

ANNALS

OF THE

MISSOURI BOTANICAL GARDEN

VOLUME 69

1982

NUMBER 1

THE SYSTEMATICS AND EVOLUTION OF *FUCHSIA* SECT. *FUCHSIA* (ONAGRACEAE)¹

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ABSTRACT

Nine sections are currently recognized in the genus *Fuchsia*, consisting of approximately 100 species. Morphological and biogeographical evidence indicates a Paleogene origin of the genus in temperate South America, with two early lines diverging to New Zealand and North America. Within South America, sects. *Quelusia* and *Kierschlegeria* have remained in the southern part of the continent, while the two largest sections, *Fuchsia* and *Hemsleyella*, have developed in the tropical Andes.

¹ Copies of this special issue of the Annals of the Missouri Botanical Garden can be obtained by sending \$7.50 per copy to Department Eleven *Studies in Fuchsia*, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166. This material is based upon research supported by the National Science Foundation under Grants No. DEB 78-05969 (to P.B.) and DEB 78-23400 (to Peter H. Raven) and is published with support of National Science Foundation Grant No. DEB-8122087. The Foundation provides awards for research and education in the sciences. The awardee is wholly responsible for the conduct of such research and preparation of the results for the publication. The Foundation, therefore, does not assume responsibility for such findings or their interpretation. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author and do not necessarily reflect the views of the National Science Foundation. A grant-in-aid from Sigma Xi helped to support the initial stages of the field work. The color illustrations and some of the figures were prepared by the Unidad de Medios Audiovisuales, Universidad Simón Bolívar, Caracas, Venezuela. The Universidad Simón Bolívar also generously covered the costs of the color plates, through the Decanato de Investigaciones. This support is gratefully acknowledged.

This study was undertaken as part of my doctoral thesis studies at Washington University, St. Louis, Missouri. I am especially thankful to Dr. Peter H. Raven for his continual interest, encouragement, and support throughout the realization of this study. The assistance of the staff and technicians of the Missouri Botanical Garden greatly facilitated my work and is strongly appreciated. I extend special thanks to Dr. Stephen S. Tillett (Herbario Ovalles, Facultad de Farmacia, Universidad Central de Venezuela) for providing advice and laboratory facilities during extended stays in Caracas, to Dr. Julian A. Steyermark (Instituto Botánico, Caracas) for his ongoing help and encouragement, and to Dr. Peter Hoch (Missouri Botanical Garden) for carefully reviewing the final draft of my thesis. My companions W. Wagner, T. P. Ramamoorthy, and J. Solomon provided helpful discussion and assistance in the preparation of this paper. The illustrations were expertly done by Eduardo Pérez; Gabriela Aedo assisted with maps and diagrams.

Many persons generously gave of their time and knowledge to assist me in the field work. I would specifically like to mention the late Dr. Luís Ruiz-Terán (Mérida, Venezuela); also, Dr. César Vargas C. (Cuzco, Peru), Dr. Ramón Ferreyra (Museo de Historia Natural Javier Prado, Lima, Peru), Dr. Abundio Sagástegui (Universidad Nacional de Trujillo, Peru), Ing^o Alberto Ortega (Universidad Nacional, Quito, Ecuador), Dr. Fernando Ortiz (Universidad Católica, Quito, Ecuador), Linda Albert de Escobar (Comisión Fulbright, Quito, Ecuador), Lic. Olga Benavides (Universidad de Nariño, Pasto, Colombia), Ing^o Eugenio Escobar (Universidad del Valle, Palmira, Colombia), Dr. Luis Mar-

This paper treats the systematics of *Fuchsia* sect. *Fuchsia*, which includes 61 species, ten of them newly described here. Despite the large number of species compared to other sections in the genus, sect. *Fuchsia* appears to be a natural grouping of species. These species all have morphological variations on a common theme, namely shrubs with tubular, reddish flowers pollinated mostly by hummingbirds. The main differences between species occur in the shape, length, or coloration of the floral tube and in the position of flowers in the leaf axils or in different kinds of racemose inflorescences.

The close relationship between species in sect. *Fuchsia* is indicated by their high level of inter-fertility with numerous naturally occurring hybrids and by chromosome numbers that are invariable or on just two levels. From over 100 new chromosome counts in populations of sect. *Fuchsia*, 37 species are now known as diploids ($n = 11$), five as tetraploids, and one species has both diploid and tetraploid populations. Chromosomal pairing in interspecific hybrids was normal in all cases examined. Naturally occurring interspecific hybrids were found in 17 different combinations, and, in two instances, populations of probable hybrid origin appear to be more successful than their local parental populations.

Altitudinal stratification of species along mountain slopes is a major isolating mechanism between different species of sect. *Fuchsia*. Though sympatry is common, species that differ substantially in floral tube length and coloration may diminish or prevent interspecific pollination by hummingbirds. Sect. *Fuchsia* possesses a particularly flexible reproductive system, combining limited vegetative reproduction with a long, essentially aseasonal flowering period in which modal outcrossing is prevalent, but autogamy also occurs.

The cool, montane habitats of the Andes presently occupied by sect. *Fuchsia* have arisen largely in the Neogene. The Andean chain actually is composed of a number of distinct structural units, each one differing somewhat in its orogeny and floristic/faunistic composition. Distributional patterns of species in the different structural units suggest that sect. *Fuchsia* has undergone a recent differentiation closely tied to the major elevation of the Andes in the Pliocene and to the glacial events and climatic fluctuations that took place during the Pleistocene. The recent diversification of most species in the section is further supported by the morphological and cytological similarities noted above, as well as by the large numbers of species in the Andes compared to other areas where *Fuchsia* occurs, and the small geographic ranges of most species there. The ability to hybridize and recombine genetic material, the presence of self-compatibility allowing establishment from a single seed after dispersal, and the recent uplift and climatic fluctuations of the Andes have probably been the key factors in the differentiation of species in *Fuchsia* sect. *Fuchsia*.

Fuchsia is a large, distinctive genus that lacks close affinities with any other group in the Onagraceae and therefore is classified as a monogeneric tribe. Its approximately 100 species are mostly mesophytic shrubs that grow in the Andes from Colombia and Venezuela to Tierra del Fuego, the southeastern coastal mountains of Brazil, Hispaniola, and the mountains of Mexico and Central America, with a small disjunct section in New Zealand and Tahiti. On the basis of chromosome number and morphology (Kurabayashi et al., 1962), floral anatomy (Eyde & Morgan, 1973), wood anatomy (Carlquist, 1975), and leaf architecture (Hickey, 1980), *Fuchsia* appears to be one of the least specialized genera in the family. In its red, tubular, bird-pollinated flowers and fleshy, bird-dispersed fruits, however, *Fuchsia* as it exists today is clearly specialized. Both *Fuchsia* and *Ludwigia*, a genus that is also relatively unspecialized and represents a phylo-

cano-Berti (Universidad de Los Andes, Mérida, Venezuela), and Dr. Gary L. Smith and Milcíades Mejía (Jardín Botánico Rafael Moscoso, Santo Domingo, Dominican Republic).

I thank the curators of the following herbaria for allowing me to examine material under their care: A, AAU, B, BH, BM, BR, BREM, CAS, CGE, CM, COL, CUZ, DS, DUKE, F, FHO, G, GH, GOET, ISC, JBSD, K, LAM, LE, LG, LIL, LL, LOJA, M, MA, MER, MERF, MICH, MO, MPU, MSC, MU, MY, MYF, NA, NY, O, OS, OXF, P, PH, POM, PR, PSO, Q, QCA, RSA, S, SIU, TCD, TEX, U, UC, UPS, US, USM, VALLE, VEN, W, WU, and Z.

Finally, my deep thanks go to my wife Eva and to Danny, who endured long separations so that this paper could be completed.

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genetic line distinct from the remainder of the family, have their center of distribution in South America, which may have been the center of origin for the family (Raven & Axelrod, 1974). In light of these relationships, an understanding of the evolutionary modes in *Fuchsia* will be fundamental to the overall understanding of evolution in the Onagraceae.

In the past 15 years, detailed systematic studies have been completed for a number of the small sections of the genus. Sect. *Encliandra* (six spp., Central America and Mexico) was revised by Breedlove (1969), sect. *Skinnera* (four spp., New Zealand and Tahiti) by E. Godley and P. H. Raven (unpublished), and finally sect. *Schufia* (two spp., Central America and Mexico) and the new sections *Ellobium* (three spp., Central America and Mexico) and *Jimenezia* (one sp., Costa Rica and Panama) by Breedlove et al. (1982). These sections, some of which present interesting developments such as male sterility and wide disjunctions in range, represent less than a fifth of the total number of species in the genus. The great majority of species of *Fuchsia* are concentrated in Andean South America, and about three-fifths of the total belong to the section treated here.

Fuchsia sect. *Fuchsia* was selected for the present revision because of its comparatively large size, with over 60 closely related species, and because it can be expected to provide a model of evolution widely applicable to other groups of the poorly studied tropical Andes. Emphasis was placed primarily on field examination of populations and morphological analysis of herbarium specimens from the major collections of the world. In this manner, the amount of hybridization and the principal isolation mechanisms operating between species could be evaluated along with morphological characters to determine more accurately species limits within the section. In addition, chromosome counts were obtained for 43 of the 61 species recognized in sect. *Fuchsia*. Concurrently with this study, an analysis of leaf flavonoids (J. Averett et al., in prep.) as well as a detailed, ultrastructural pollen survey of the entire genus (J. Nowicke et al., in prep.; J. Praglowski et al., in prep.) are nearing completion, and systematic studies are underway in the remaining three sections from South America, *Quelusia*, *Kierschlegeria* and *Hemsleyella* (P. E. Berry and T. P. Ramamoorthy, in prep.).

ORIGIN OF THE GENUS AND SUBGENERIC RELATIONSHIPS

AGE AND RELATIONSHIPS OF *FUCHSIA*

Despite the unequivocal familial limits of the Onagraceae, no clear relationships are apparent between the seven tribes in the family. Although no tribe presents a series of features that can be considered ancestral to the rest, *Ludwigia*, the sole genus of the Jussiaeae, is the most distinct and clearly represents an early offshoot of the family (Raven, 1979a). The other six tribes are therefore more closely related to one another than any one is to *Ludwigia*. The monogeneric tribe Fuchsiae is the tribe with the largest assemblage of unspecialized features, including the absence of interxylary phloem and unspecialized chromosomes and placentation (Eyde & Morgan, 1973).

The order Myrtales, to which the Onagraceae belong, is clearly a southern hemisphere group (Raven & Axelrod, 1974). *Ludwigia* has its least specialized

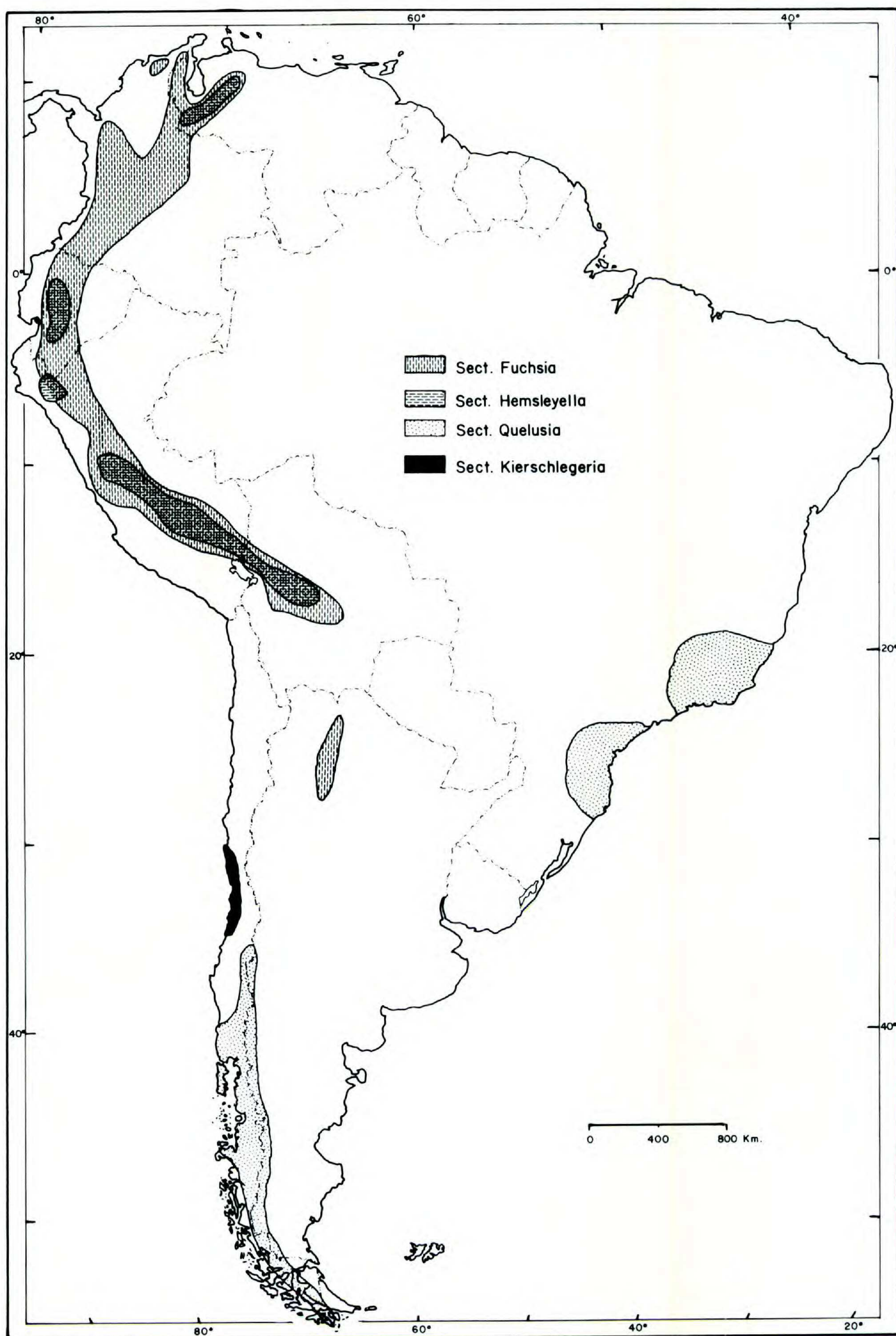
TABLE 1. Main historical subdivisions of *Fuchsia*.

Author	Equivalent Modern Sections ¹
DECANDOLLE (1828)	
Sect. <i>Quelusia</i>	
<i>Breviflorae</i>	<i>Encliandra</i> , <i>Kierschlegeria</i>
<i>Macrostemonae</i>	<i>Fuchsia</i> (part), <i>Quelusia</i> , <i>Schufia</i>
<i>Longiflorae</i>	<i>Fuchsia</i> (part), <i>Hemsleyella</i> , <i>Ellobium</i>
Sect. <i>Skinnera</i>	<i>Skinnera</i>
ENDLICHER (1840)	
a. <i>Encliandra</i> ²	
<i>Brebissonia</i>	<i>Encliandra</i> (part)
<i>Lyciopsis</i>	<i>Encliandra</i> (part)
b. <i>Fuchsia</i> ²	
<i>Kierschlegeria</i>	<i>Kierschlegeria</i>
<i>Fuchsia</i>	<i>Fuchsia</i> , <i>Quelusia</i>
<i>Schufia</i>	<i>Schufia</i>
c. <i>Skinnera</i> ²	<i>Skinnera</i>
HEMSLEY (1877)	
“American species having petals”	
Tropical Andean species	<i>Fuchsia</i>
Brazilian species	<i>Quelusia</i> (part)
South Andean species	<i>Quelusia</i> (part), <i>Kierschlegeria</i>
Mexican and Central American species	<i>Encliandra</i> , <i>Schufia</i> , <i>Ellobium</i>
“American species destitute of petals”	<i>Hemsleyella</i>
“New Zealand species”	<i>Skinnera</i>
MUNZ (1943)	
Sect. <i>Quelusia</i>	<i>Quelusia</i>
Sect. <i>Fuchsia</i>	<i>Fuchsia</i> , <i>Ellobium</i> (part)
Sect. <i>Kierschlegeria</i>	<i>Kierschlegeria</i>
Sect. <i>Skinnera</i>	<i>Skinnera</i>
Sect. <i>Hemsleyella</i>	<i>Hemsleyella</i> , <i>Ellobium</i> (part)
Sect. <i>Schufia</i>	<i>Schufia</i>
Sect. <i>Encliandra</i>	<i>Encliandra</i>

¹ Includes only groups or species known at the time of publication.

² Groups of undesignated rank, but subsequently taken up as sections by Walpers (1843), Benth & Hooker (1867), and Baillon (1877).

members and greatest species diversity in South America, as well as all of its self-incompatible species. *Fuchsia* likewise has by far its greatest concentration of species in South America and had reached New Zealand by the latest Oligocene (Mildenhall, 1980). Because of these relationships, it has been hypothesized that the Onagraceae originated in South America (Raven & Axelrod, 1974; Raven, 1979a). All of the remaining tribes of the family, however, have their centers of diversity in the northern hemisphere, and fossil pollen of *Ludwigia* is known from the northern hemisphere from the early Paleogene onward (Eyde & Morgan, 1973). Thus very early dispersal between the two hemispheres clearly occurred. The Onagraceae originated by the close of the Cretaceous (Raven & Axelrod, 1974); earliest fossil remains assignable to genera are from the Paleocene for *Ludwigia* and the Oligocene for *Circaea*. The earliest fossil record for *Fuchsia*

FIGURE 1. Native distributions of the South American sections of *Fuchsia*.

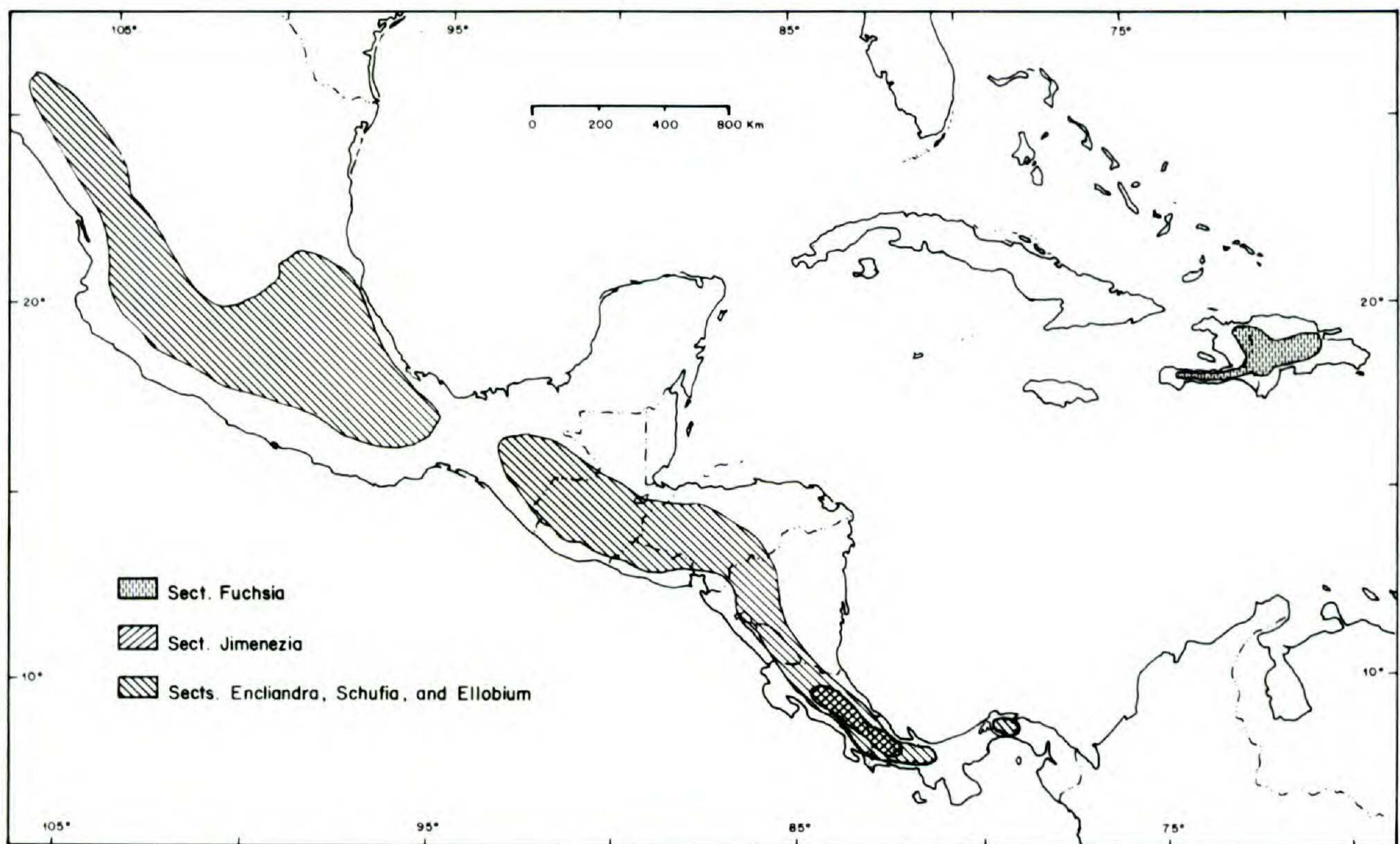


FIGURE 2. Native distributions of the sections of *Fuchsia* outside of South America, not including sect. *Skinnera*, which is endemic to New Zealand and Tahiti.

is pollen from the uppermost Oligocene of New Zealand (Couper, 1960; Mildenhall, 1980), which gives us a minimum age for the genus. Because of the possession of a number of advanced characters, the New Zealand species of *Fuchsia* are almost certainly derived from American ancestors, so the genus probably evolved considerably earlier. Bird pollination is a dominant theme in *Fuchsia* and is present in both New World and Old World groups; the fruits are also adapted to bird dispersal. Specialized flower-visiting birds probably did not evolve until the Eocene (Sussman & Raven, 1978), but it is uncertain whether the common ancestor of *Fuchsia* would have been bird-pollinated or not. At any event, plants similar to the existing species of *Fuchsia* probably could not have evolved prior to the Eocene. The most likely hypothesis, therefore, is that the genus originated in the Eocene or Oligocene in South America.

SUBGENERIC TREATMENTS OF *FUCHSIA*

Attempts to recognize several related genera in the tribe Fuchsieae, such as Spach's (1835) treatment, have met with little acceptance because of the existence of intermediate taxa linking the most divergent species and because of the lack of fundamental differences in the basic features of the group. In contrast, a number of infrageneric groups have traditionally been recognized as sections or as groups of undesignated rank. A synopsis of the different subgeneric treatments of *Fuchsia* until Munz's (1943) generic monograph is listed in Table 1.

DeCandolle (1828) divided the genus into sect. *Skinnera*, from New Zealand, and sect. *Quelusia*, from America. He based his subdivisions of sect. *Quelusia* on the degree of staminal exsertion and the relative length of the floral tube and

TABLE 2. The sections of *Fuchsia* and their native geographical distribution.

Section	Estimated number of Species	Distribution
1. <i>Quelusia</i>	5	SE coastal Brazil, Chile & Argentina
2. <i>Fuchsia</i>	61	Tropical Andes, Hispaniola
3. <i>Ellobium</i>	3	Mexico and Central America
4. <i>Hemsleyella</i>	14	Tropical Andes
5. <i>Kierschlegeria</i>	1	Central coastal Chile
6. <i>Schufia</i>	2	Mexico and Central America
7. <i>Jimenezia</i>	1	Panama and Costa Rica
8. <i>Encliandra</i>	6	Mexico and Central America
9. <i>Skinnera</i>	4	New Zealand and Tahiti
TOTAL:	97	

sepals. His subdivisions represent what now seems to have been an unnatural division of the presently recognized sections. Endlicher (1840) made a few improvements over DeCandolle's treatment, such as the segregation of the distinctive *Schufia* group and the separation of *Kierschlegeria* from *Encliandra*. Despite Hemsley's (1877) informal style of presentation, his arrangement is remarkably close to our modern sectional concepts of the genus. Through his geographical criteria and familiarity with living, introduced species, Hemsley first recognized the integrity of the modern sects. *Fuchsia*, *Hemsleyella*, and, in part, *Quelusia*. Finally, Munz's (1943) generic revision ordered the previous diverse subgeneric concepts into a consistent, formal system consisting of seven sections.

Recent study of the Mexican and Central American species of *Fuchsia* has introduced several changes into Munz's sectional classification (Breedlove et al., 1982). The currently recognized sections are listed along with their native distribution and species numbers in Table 2, and maps of their distributions appear in Figures 1 and 2.

KEY TO THE SECTIONS OF *FUCHSIA*

- 1a. Petals lacking or much reduced, if present, less than one third the length of the sepals and with floral tubes 5–15 mm long; leaves generally alternate.
 - 2a. Floral tube 5–15 mm long; gynodioecious or dioecious; leaves usually present when flowering; New Zealand and Tahiti. sect. *Skinnera*
 - 2b. Floral tube 17–170 mm long; hermaphroditic; often flowering when leafless; South America. sect. *Hemsleyella*
- 1b. Petals present, usually conspicuous and more than one third the length of the sepals, if shorter, with floral tubes 20–130 mm long; leaves generally opposite or whorled.
 - 3a. Antepetalous stamens reflexed and included in the floral tube.
 - 4a. Flowers axillary, dioecious or subdioecious; berries with 6–35 seeds; Mexico to Panama. sect. *Encliandra*
 - 4b. Flowers in terminal racemes or panicles, hermaphroditic; berries with 35–80 seeds; Costa Rica and Panama. sect. *Jimenezia*
 - 3b. Stamens all erect and exserted beyond the floral tube.
 - 5a. Small trees; flowers numerous, erect in well-developed di- or trichotomously branched panicles. sect. *Schufia*
 - 5b. Shrubs, climbers, or epiphytes, rarely arborescent; flowers spreading or pendant and axillary, racemose, or in few-branched panicles.
 - 6a. Petiole bases persisting as woody, spinose knobs on the stem; subdioecious; floral tube 3–10 mm long and sepals reflexed; berries with 14–30 seeds. sect. *Kierschlegeria*

- 6b. Petioles dehiscing flush with the stem and never spinose; hermaphroditic; floral tube 10–130 mm long or, if shorter, sepals not reflexed; berries with 30–250 seeds.
- 7a. Floral tubes usually shorter than the sepals, these $\pm$ connate at the base; stamens exerted well beyond the sepals; petals convolute after anthesis; flowers axillary; Southern Andes and southeast Brazil (introduced elsewhere). ----- sect. *Quelusia*
- 7b. Floral tubes usually longer than the sepals, if not, with sepals free to the base; stamens generally not exerted beyond the sepals, petals not overlapping at anthesis; flowers axillary, racemose, involucrate, or paniculate; Central Andes to Mexico and Hispaniola.
- 8a. Leaves mostly opposite, broad, elliptic-ovate or cordate; tubers present, or plants epiphytic, if not, with green petals; nectary a smooth, unlobed band lining the base of the tube; Central America and Mexico. ----- sect. *Ellobium*
- 8b. Leaves opposite to whorled, variously shaped but generally not cordate at the base; tubers lacking; plants terrestrial, the petals never green; nectary annular and mostly free from the base of the tube or with prominent lobes adnate to it; South America and Hispaniola (introduced elsewhere). ----- sect. *Fuchsia*

INTERSECTIONAL RELATIONSHIPS AND EVOLUTIONARY LINES IN *FUCHSIA*

As discussed previously, *Fuchsia* probably originated in South America. The genus almost invariably occurs in cool, mesic climates and is centered in tropical uplands or temperate forest below the frost zone. The three main ecogeographic areas of South America occupied by *Fuchsia* are 1) cloud forests of the tropical Andes, 2) *Nothofagus* forest in the temperate Andes, and 3) montane forest in southeastern Brazil. The floristic relationships of these three areas have been pointed out by numerous authors, including Gerth (1941), Smith (1962), and Vuilleumier (1969), based on such diverse taxa as *Araucaria*, *Drimys*, *Berberis*, *Lepechinia*, *Podocarpus*, *Ilex*, *Chusquea*, and *Perezia*. These elements are considered to be remnants of ancient, widely distributed temperate forests across southern South America (Simpson, 1973, 1979). Paleontological, paleoclimatic, and geological evidence indicates that a generally warm and equable climate prevailed throughout South America in the early Tertiary, with tropical rainforest vegetation extending considerably farther south than at present (see reviews in Vuilleumier, 1969; Simpson 1973, 1979; Haffer, 1974; Solbrig, 1976; Duellman, 1979). Fossil evidence of fully tropical wet forest is known from the Eocene in Argentina at 38°S, with subtropical woods and pampa occurring at 42°S. A marked cooling and drying trend began in the Oligocene and Miocene, however, with the result that temperate elements of the Antarcto-Tertiary Geoflora migrated farther north, replacing the tropical flora of Chile and Argentina. In the Oligocene, austral forests of *Nothofagus*, *Araucaria*, and *Laurelia* were present as far north as 30°S in Argentina (Jeannel, 1967). Subsequently the continuity of this continuous forest was broken up by the rain shadows created by the rising Andes and by the spread of the Tertiary-Chaco Geoflora (Solbrig, 1976). The fragmentation of the once widespread southern forests continued, and by the Pliocene most of the *Nothofagus* forests east of the Andes had disappeared completely.

Given this background, we may hypothesize that the ancestral stock of *Fuchsia* evolved within the southern temperate forests of South America during the Eocene or Oligocene. Several main lines of the genus probably diverged in the

late Oligocene and Miocene, when the austral forests began to contract and fragment, and the Andes began to be uplifted substantially. One of the earliest offshoots of *Fuchsia* was sect. *Skinnera*. As indicated by pollen fossils (Mildenhall, 1980), *Fuchsia* was present in New Zealand, where there are three very distinct species of sect. *Skinnera*, by the late Oligocene. It probably spread across Antarctica, contrary to the earlier view of Raven, who postulated a long distance dispersal route across the Pacific (Raven, 1972a, p. 242). At that time, *Fuchsia* had not been reported from New Zealand prior to the middle Miocene, and it was not understood that more or less direct opportunities for migration across Antarctica persisted until the Miocene (Raven, 1979b). The fourth species of sect. *Skinnera*, *F. cyrtandroides*, is endemic to the Pacific island of Tahiti, which is of volcanic origin and less than two million years old (Dymond, 1975). This species undoubtedly arrived there from New Zealand by long distance bird transport, since the entire Tahitian flora is adapted to long distance dispersal, and nearly 40% of the plant species there are adapted to internal transport by birds (Carlquist, 1967). Members of sect. *Skinnera* are probably better adapted to long distance transport than are other sections of the genus because they have the smallest and most numerous seeds (up to 450 per fruit) in the genus.

Other distinctive characters reflect the early divergence of sect. *Skinnera*. Initial results of a survey of leaf flavonoids in the genus indicate that it is the only section with what appears to be sulfated flavonoids (J. Averett et al., in prep.). It also includes the most widely divergent growth forms in the genus—procumbent creepers, lianas, and tall trees. A strong reduction of petals occurs in the section, and it has smooth, band-type nectaries like those of sects. *Hemsleyella* and *Ellobium* and beaded viscin threads on the pollen as in all South American sections except sect. *Kierschlegeria*.

Another offshoot probably spread early in the history of the genus to North America by long distance dispersal, most likely in Paleogene time. Other families that show this pattern of an early South to North American migration include Cactaceae, Loasaceae, Nyctaginaceae, and Zygophyllaceae (see Raven & Axelrod, 1974, pp. 627 and 628 for more complete lists). This early offshoot of *Fuchsia* that reached North America eventually differentiated into the modern sects. *Encliandra*, *Jimenezia*, and *Schufia*. Though each one of these sections is now quite distinct from each other, common ancestry is suggested by the following shared characters: smooth viscin pollen threads (though a few intermediate types occur in sect. *Encliandra*), small flowers adapted to insect pollination in several species, and similar lobed-adnate nectaries. Other derived characters are the presence of male sterility in sects. *Encliandra* and *Schufia*, antepetalous stamens reflexed into the floral tube in sects. *Encliandra* and *Jimenezia*, and low seed or ovule number in sect. *Encliandra*. Sections *Encliandra* and *Schufia* have their center of diversity in Mexico and only secondarily spread south of the Isthmus of Tehuantepec (Breedlove, 1969; Breedlove et al., 1982). Section *Jimenezia*, clearly closely related to, but more primitive than, sect. *Encliandra*, is monotypic and endemic to a small area of Costa Rica and Panama.

The remaining sections represent the majority of the species in the genus; they probably arose from a common ancestor as the austral temperate forests of South America became increasingly limited in area and the Andes were uplifted

during the Miocene and Pliocene. Sections *Quelusia*, *Fuchsia*, *Hemsleyella*, and *Ellobium* are all basically hummingbird-pollinated, hermaphroditic, and have similar beaded viscin pollen threads. They differ in characters such as nectary type, petal size, ploidy level, pollen pore number, and habit, however. Because sect. *Quelusia* inhabits areas in southeastern Brazil and Chile-Argentina that are more directly related to the ancient austral temperate forests than are the areas of the remaining sections, we may infer that its relatively short floral tubes and exerted stamens are more primitive characters than the long tubes characteristic of the other sections. Simpson (1973) presented extensive biogeographical evidence that the present day South American *Nothofagus* forests are refuges for many taxa that may have been present and have changed little since the early to mid-Tertiary. Section *Quelusia* is entirely polyploid and may have retained certain primitive characters for this reason. As Simpson pointed out for other taxa, relatively little differentiation seems to have occurred in the *Nothofagus* forests compared to related species elsewhere. A single widespread species of *Fuchsia*, *F. magellanica*, is found in these forests today. In contrast, the remaining species of sect. *Quelusia* in southeastern Brazil have radiated strongly there, as have many other plant groups (see Smith, 1962, and Plowman, 1979, for examples).

Section *Kierschlegeria* consists of a single species, *Fuchsia lycioides*, that grows in the summer-dry coastal vegetation of central Chile. This is the only species in the genus that occupies a seasonally dry habitat, and it has evolved a series of xeromorphic adaptations such as small, deciduous leaves, spinose leaf bases, and thick seed coats. The habitats where it occurs did not exist before the Pleistocene, when the Andes reached their present elevation and the cold Humboldt Current brought on greatly increased aridity to the Pacific coast of south-central South America (Raven, 1973; Simpson, 1975a; Solbrig, 1976). Notwithstanding this, it probably began to evolve its peculiar constellation of characters earlier in local pockets of aridity at the margins of the tropics. The lobed-adnate nectaries, triporate pollen grains, and tetraploidy make a common origin with sect. *Quelusia* seem likely, especially in view of the geographical proximity of these groups. *Fuchsia lycioides* is dioecious (Atsatt & Rundel, 1982) and its low ovule number and conceivably even its smooth viscin threads might be specializations related to this aspect of its breeding system. It seems possible that the three-pored pollen characteristic of these sections and present in all genera of Onagraceae other than *Fuchsia*, might be a shared primitive characteristic of sects. *Quelusia* and *Kierschlegeria*, and not directly related to their polyploid nature.

Sections *Fuchsia* and *Hemsleyella* are sympatric and restricted to the moist slopes of the tropical Andes, except for two disjunct species of sect. *Fuchsia* on Hispaniola, in the West Indies. The ancestors of these two sections probably migrated northward from the austral temperate forests in South America into new, cool, montane habitats that began to develop on the eastern slopes of the central Andes as they began to rise during the Miocene. Large areas of cool Andean forest probably did not exist until the Pliocene, however, when the major uplift of the Andes occurred. Section *Fuchsia* occurs in aseasonal habitats and is petaloid and mostly diploid; most species have a particular annular nectary (see Figs. 42 and 43). Section *Hemsleyella*, in which polyploidy is more frequent, is apetalous and has evolved a series of seasonal adaptations linked to a predom-

inantly epiphytic habit. Members of this section usually live on rocks or trees that are subject to much higher water stress than plants of sect. *Fuchsia* that grow in moist soil nearby. Most species of sect. *Hemsleyella* have developed adaptations such as thick, tuberous stems and dry season flowering and leaf drop.

Section *Ellobium* was recently segregated from sects. *Fuchsia* and *Hemsleyella* and includes three species in Mexico and Central America (Breedlove et al., 1982). Despite its northern range, sect. *Ellobium* has clear South American affinities and is morphologically intermediate between sects. *Fuchsia* and *Hemsleyella*, having petals as in sect. *Fuchsia* and band nectaries as in sect. *Hemsleyella*. A clear specialization trend occurs in the section from a nontuberous, mostly aseasonal species with large petals to a strongly seasonal, tuberous, epiphytic, and nearly apetalous species. Unlike the sympatric sections *Schufia* and *Encliandra*, the most generalized species of sect. *Ellobium* occur from Costa Rica to Mexico, while the more specialized ones are restricted to Mexico. This distribution pattern and the probable young age of the related sects. *Fuchsia* and *Hemsleyella* indicates that sect. *Ellobium* reached Central and North America by an independent dispersal event from South America. Most likely, the ancestors of sect. *Ellobium* reached the high mountains of Costa Rica once the Pliocene land connection between North and South America was established, then differentiated farther north into seasonally drier habitats.

Summarizing, the most primitive existing sections of *Fuchsia* may be *Quelusia* and *Kierschlegeria*, of temperate habitats in southern South America. The ancestors of sect. *Skinnera* reached New Zealand from temperate South America prior to the close of the Oligocene. The common ancestor of the North American sections *Jimenezia*, *Encliandra*, and *Schufia* likewise may have been derived from antecedents that occurred in the Paleogene of temperate South America and reached similar habitats in North America. Generalized features for the genus may be sought by comparing characteristics common to these main groups. The differentiation of the more modern and related sections *Fuchsia*, *Hemsleyella*, and *Ellobium* in the Andes and, ultimately, North America, seems definitely to have been a Neogene phenomenon linked with the uplift of the Andes and the diversification of suitable habitats there, as well as with floral specialization to hummingbird pollination. The rest of this paper deals with the systematics and evolution of sect. *Fuchsia* and is aimed at analyzing how this particular line of the genus was able to differentiate so extensively in a relatively short time span. The patterns of evolution in this section should serve to illustrate comparable patterns in many other groups that inhabit the same areas, and that have been derived from diverse sources.

ECOLOGY AND GEOGRAPHICAL DISTRIBUTION

ECOLOGY

Habitat. Plants of *Fuchsia* sect. *Fuchsia* typically occupy moist, semidisturbed habitats of cool, montane forest. In the Andes this vegetation zone is commonly referred to as "cloud forest," but locally other terms are used such as "yungas" (Bolivia), "ceja" (Peru and Ecuador), and "montaña" (northern Andes). Lauer (1979) calls this formation the "tropical upper montane forest."



FIGURES 3-4. Habitats of *Fuchsia* sect. *Fuchsia* in the Andes.—3. Habitat of *F. venusta*, on the edge of a patch of cloud forest at 2,400 m in Dept. Tolima, Colombia. Arrow points to the position of flowering branches of *F. venusta*, found growing as a liana here. It also occurs as an erect or scandent shrub.—4. Habitat in which *F. venusta* (Berry 3455), *F. nigricans* (Berry 3454), and a hybrid between them (Berry 3453) were found growing together, between La Carbonera and La Azulita, 2,220 m, Edo. Mérida, Venezuela.



According to the Holdridge life zone system, the habitats of *Fuchsia* correspond to the humid, very humid, or pluvial montane or low montane life zones (Ewel et al., 1976). Three of Cuatrecasas' (1958) vegetation zones in Colombia are inhabited by *Fuchsia*, the upper part of the Subandean Forest (ca. 1,000–ca. 2,400 m), the Andean Forest (ca. 2,400–ca. 3,400 m), and the Subpáramo (ca. 3,400–ca. 4,000 m). Unlike the discontinuous and physiognomically distinct wet montane formations in much of Central America (oak–pine, mixed broadleaf forests), the cloud forests of the tropical Andes are essentially continuous on the eastern slopes from 12°N to 27°S latitude and are difficult to separate into distinct physiognomic units (Simpson, 1979).

The two main ecophysiological requirements of sect. *Fuchsia* are ample light and high, constant soil moisture. As shown by the long, wide vessel elements in the xylem and the lack of interxylary phloem (Carlquist, 1975), *Fuchsia* is clearly adapted to strongly mesic conditions. Because of their moderately high light requirements, plants of sect. *Fuchsia* are rarely found in tall or heavily shaded forests; the few plants that I have seen in such habitats were climbers that had reached the canopy or a light break in the forest (Fig. 3). Although seeds of *Fuchsia* germinate in the light, the inability of most species to withstand even moderate water stress prevents them from growing in open or strongly disturbed sites such as clearings or pastures. Many species of sect. *Fuchsia* are found growing in wet soil or near moving water, and they are typically found in thickets formed along road cuts or forest edges. In areas where human interference has

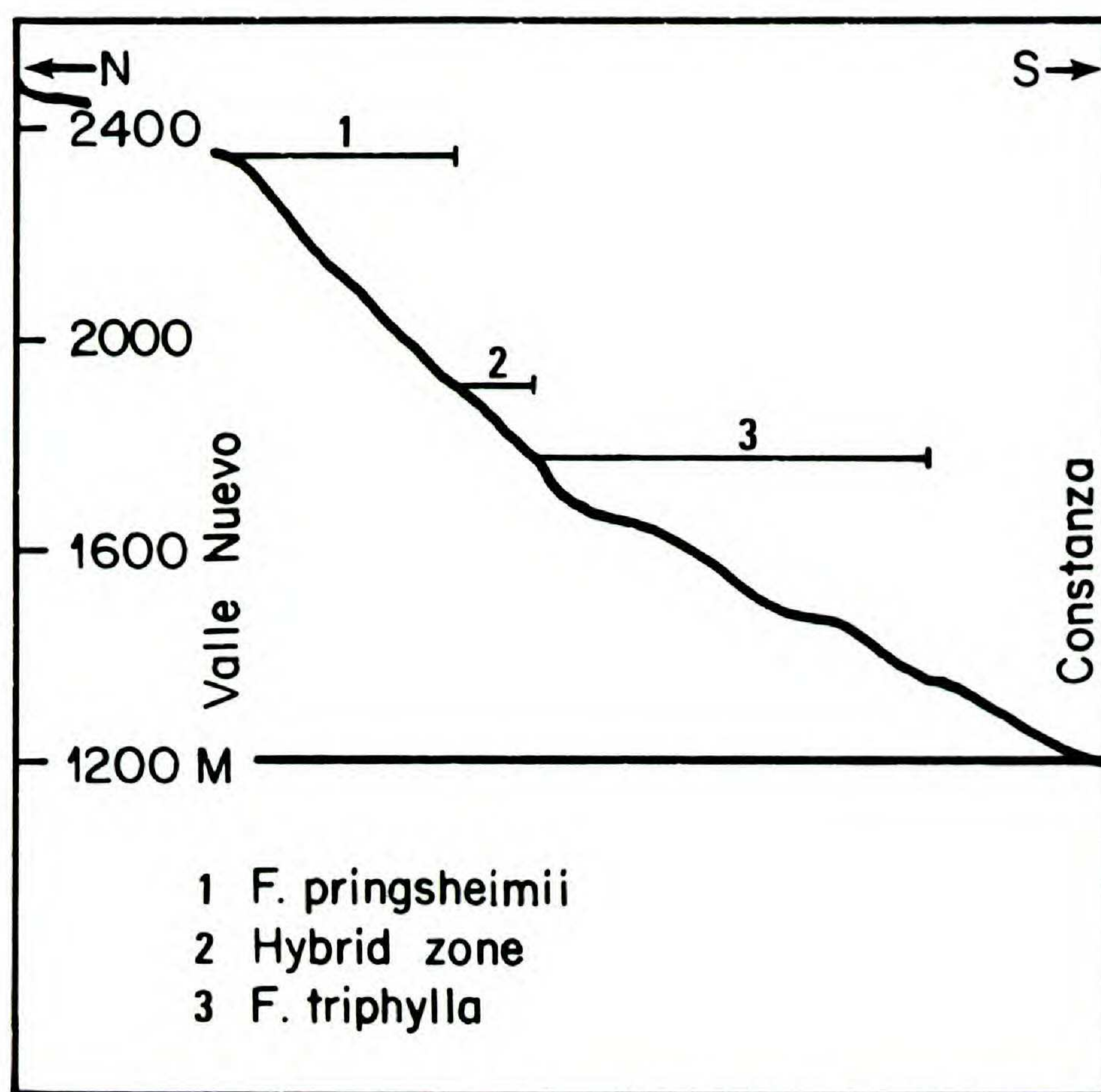


FIGURE 5. Altitudinal zonation of *Fuchsia* along a transect in Prov. La Vega, Dominican Republic.

been minimal, *Fuchsia* is found in naturally disturbed sites that can be fairly widespread on the steep slopes of wet forest, including treefalls, landslides, and streamsides. Larger populations are found in more open areas, however, so that a limited amount of human disturbance such as occasional clearings and road cuts seems to promote the growth and expansion of populations of most species in sect. *Fuchsia* (Fig. 4).

A few species occur outside of the cloud forest belt, either near its upper or lower limits or in drier formations. The *Fuchsia petiolaris* species group occurs at high elevations near the upper cloud forest limits and sometimes even extends into the páramo (Cleef, 1979). *Fuchsia vulcanica* is found at 4,000 m in northern Ecuador and southern Colombia, but *Fuchsia macrophylla* extends down into the subtropical forest at 1,200 m in central and southern Peru. *Fuchsia triphylla*, an endemic on Hispaniola, is exceptional in that it occasionally grows in open fields and also occurs as low as 1,000 m. Both *F. loxensis* and *F. dependens* are found in the high, rain-shadowed central valley of Ecuador, where they are usually found as mostly erect shrubs in hedgerows. *Fuchsia denticulata* is the only species in the section that inhabits the dry Pacific slopes of central Peru; it lives there in moist canyons mostly as an erect shrub, whereas the same species is a sprawling shrub or climber in cloud forests on the eastern slopes. The only widely naturalized species in the section, the arborescent *F. boliviana*, is tolerant of open habitats with moderate moisture stress, occupying a wider range of climatic conditions than most other species in the group.

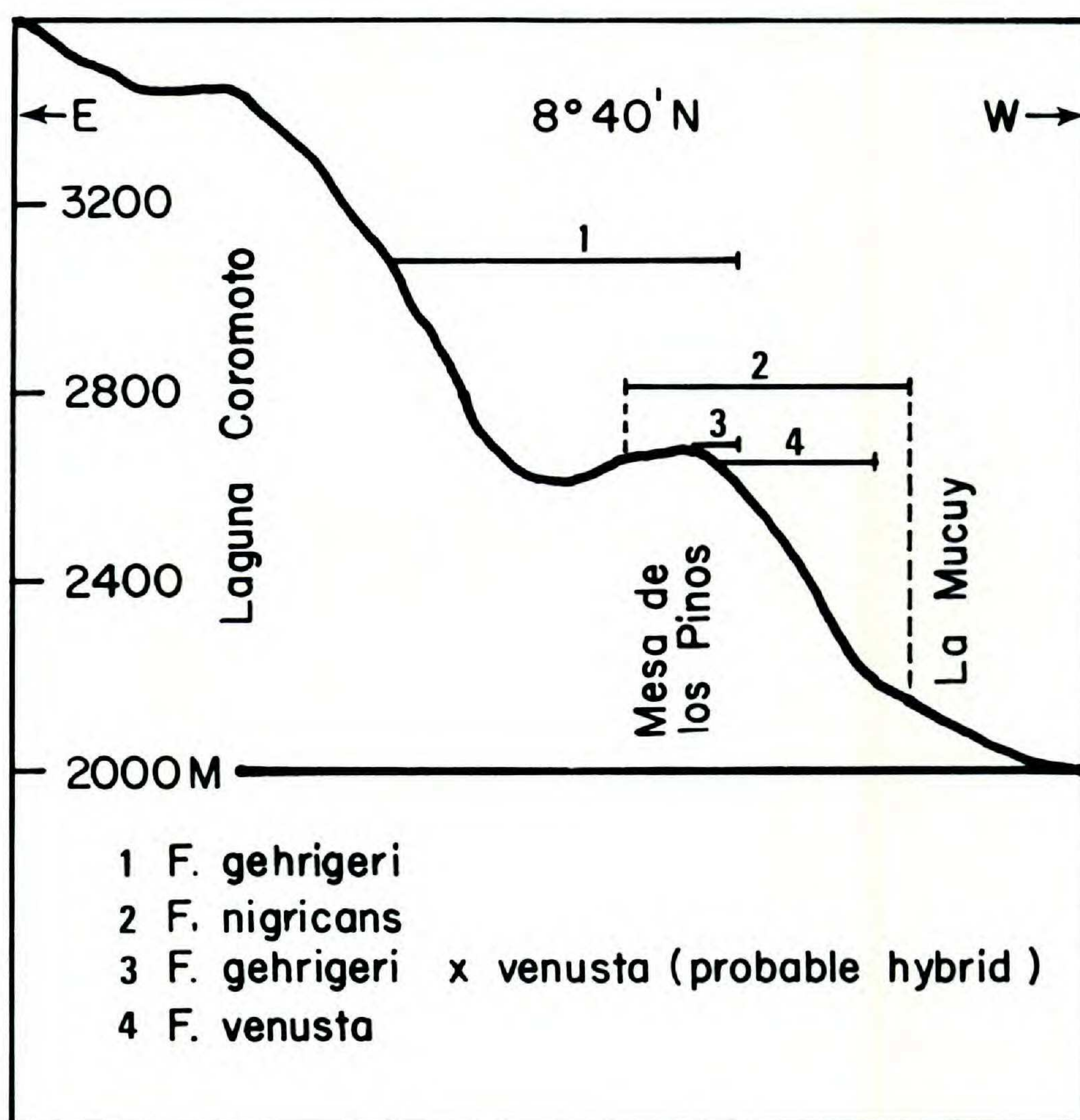


FIGURE 6. Altitudinal zonation of *Fuchsia* along a transect on the west slopes of the Sierra Nevada de Mérida, Edo. Mérida, Venezuela.

Altitudinal separation of species. Many species within sect. *Fuchsia* have different elevational tolerances, and the altitudinal stratification of species on the same mountain system is one of the principal isolating mechanisms operating between species. Hybrids are most often found where the altitudinal limits of partially sympatric species overlap. Figures 5 to 11 illustrate several examples of the successive altitudinal replacement of species on the same mountain range, which is found throughout the range of the section. The figures are based on data from field studies and herbarium specimens.

Phenology. Data from collection dates of herbarium specimens and field observations of populations of several species indicates that very little periodicity occurs in the flowering or appearance of new leaves in sect. *Fuchsia*. All the species are evergreen, and senescent leaves gradually fall off the older stems and are replaced by new leaves on the young axillary or terminal shoots. Individuals or local populations of *F. boliviana*, *F. dependens*, *F. nigricans*, and *F. venusta* are known to flower throughout the entire year.

Though annual temperature variation in the Andean cloud forests is slight, especially compared to the daily fluctuations, precipitation is seasonal, with one

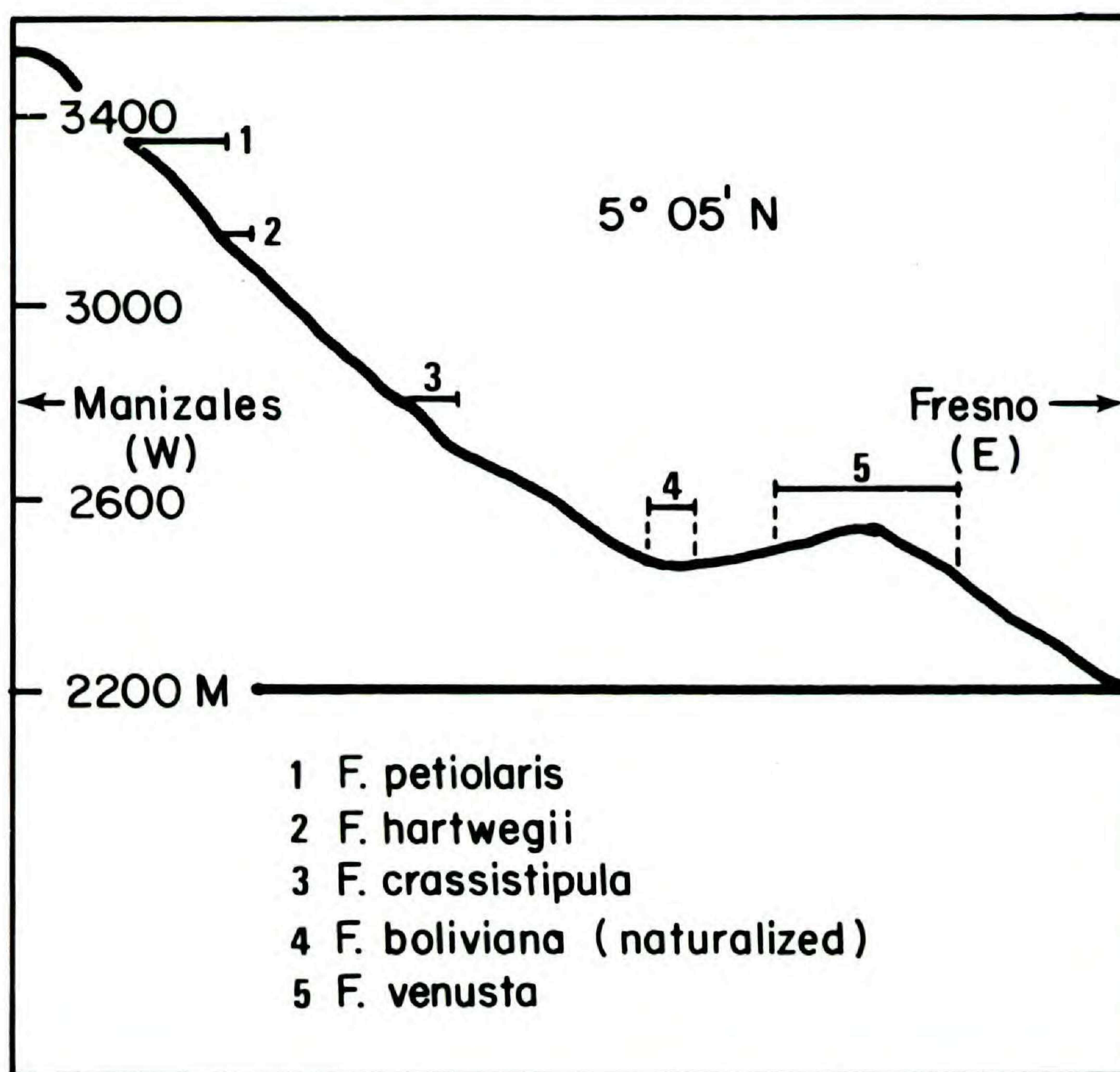


FIGURE 7. Altitudinal zonation of *Fuchsia* along a transect on the east slopes of the Cordillera Central in Dept. Tolima, Colombia.

or two relative dry seasons in different latitudes (Simpson, 1979). Definite growth cycles and periodicity in leaf and flower production occur in the sympatric sect. *Hemsleyella*. These plants, however, are mostly epiphytic or grow on rocks, where they are subject to much greater water stress, especially in drier periods. Members of sect. *Fuchsia* rarely experience a water deficit because they are terrestrial and grow in semi-shaded sites with high year-round soil moisture.

Section *Fuchsia* employs a "steady-state" flowering strategy (Gentry, 1974), whereby relatively few flowers are produced over an extended time period (usually a month or two). This strategy is adapted to pollinators with fixed foraging patterns such as bees and hummingbirds. It is important to note, however, that although pollination efficiency may be heightened by this strategy, temporal separation of flowering periods can *not* be an operative reproductive isolation mechanism in sect. *Fuchsia*.

GEOGRAPHICAL DISTRIBUTION

Geological background of the Andes. The Andes are a classic example of a mountain range that has a volcano-plutonic origin along a convergent plate margin (Sillitoe, 1974). As outlined in recent reviews of the Andean orogeny (Hammen, 1974; Haffer, 1974; Sillitoe, 1974; Simpson, 1975b, 1979; Flenley, 1979) three events in the history of the Andes have been of key importance to the develop-

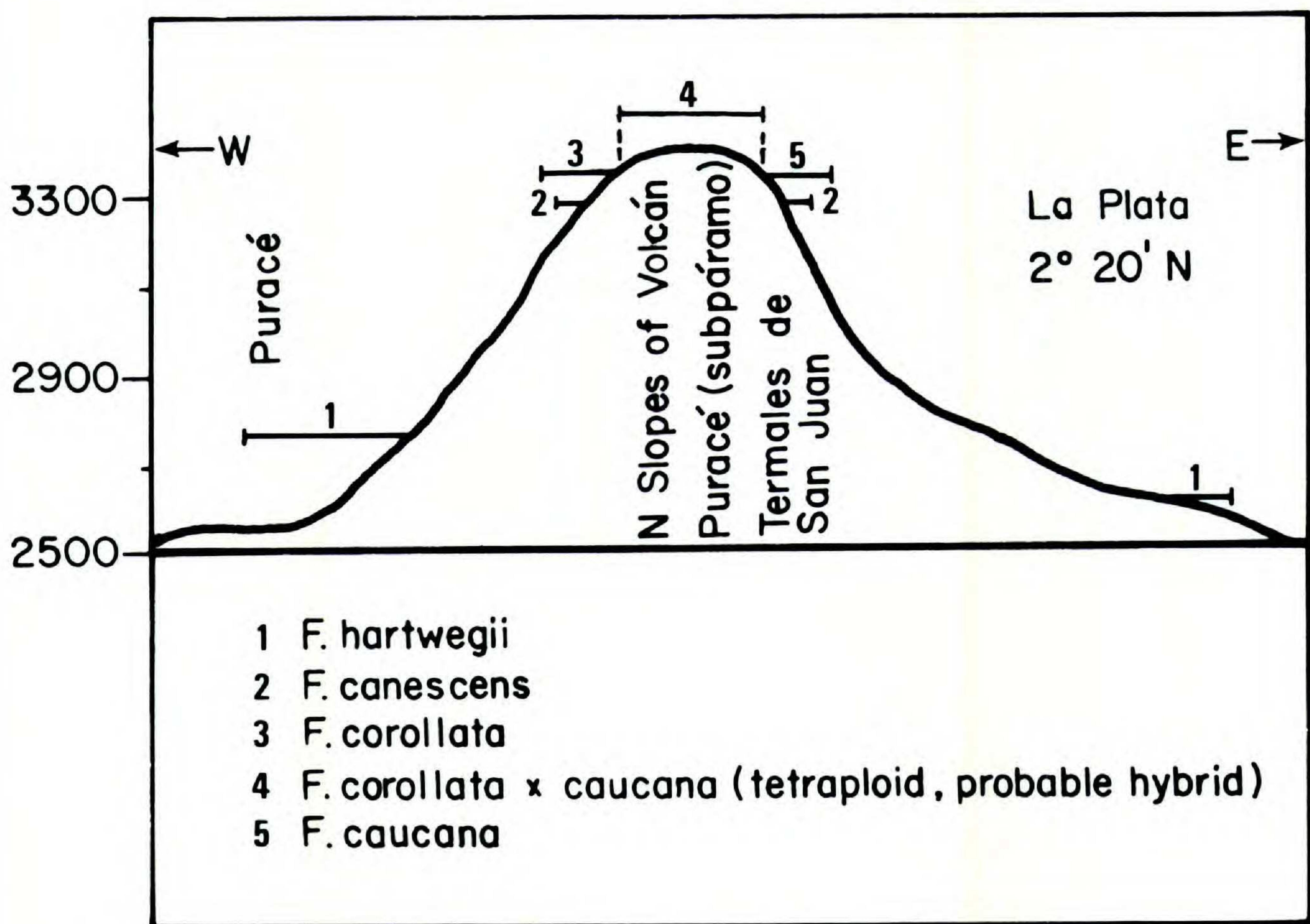


FIGURE 8. Altitudinal zonation of *Fuchsia* along a transect crossing the Cordillera Central in Depts. Cauca and Huila, Colombia.

ment of the native flora there. First, the final and major uplift throughout the Andes, accounting for an average 2,000–3,000 m increase in elevation, occurred toward the end of the Pliocene. As Hammen (1979) states, this implies that, at least in the northern Andes, the history of the Andean forest vegetation zone dates from the upper Miocene or lower Pliocene, while the páramo flora can only be traced back to the mid- to upper Pliocene. The youth of the high Andean flora is further demonstrated by the absence of endemic plant families in the páramos and by the low number of endemic páramo genera (Cleef, 1979).

Second, geomorphological and tectonic evidence indicates that, rather than having a longitudinally continuous orogeny, the Andes are actually composed of a number of separate, longitudinal segments (Fig. 12). The boundaries between these segments usually coincide with major changes in overall geology, strike, or even width of the Andes, and each segment represents a different piece of lithosphere that was individually subducted at probably different rates. The particular history of each segment affected its faunistic and floristic composition, and analyses such as those of Simpson (1975b) and Duellman (1979) have shown that distributions of Andean forest species tend to coincide with the basic geological discontinuities between structural units.

Finally, the Andes, as well as lowland tropical South America, were strongly affected during the Pleistocene by the same glacial cycles that drastically altered the climates of the temperate regions of the world. One to four major glaciations

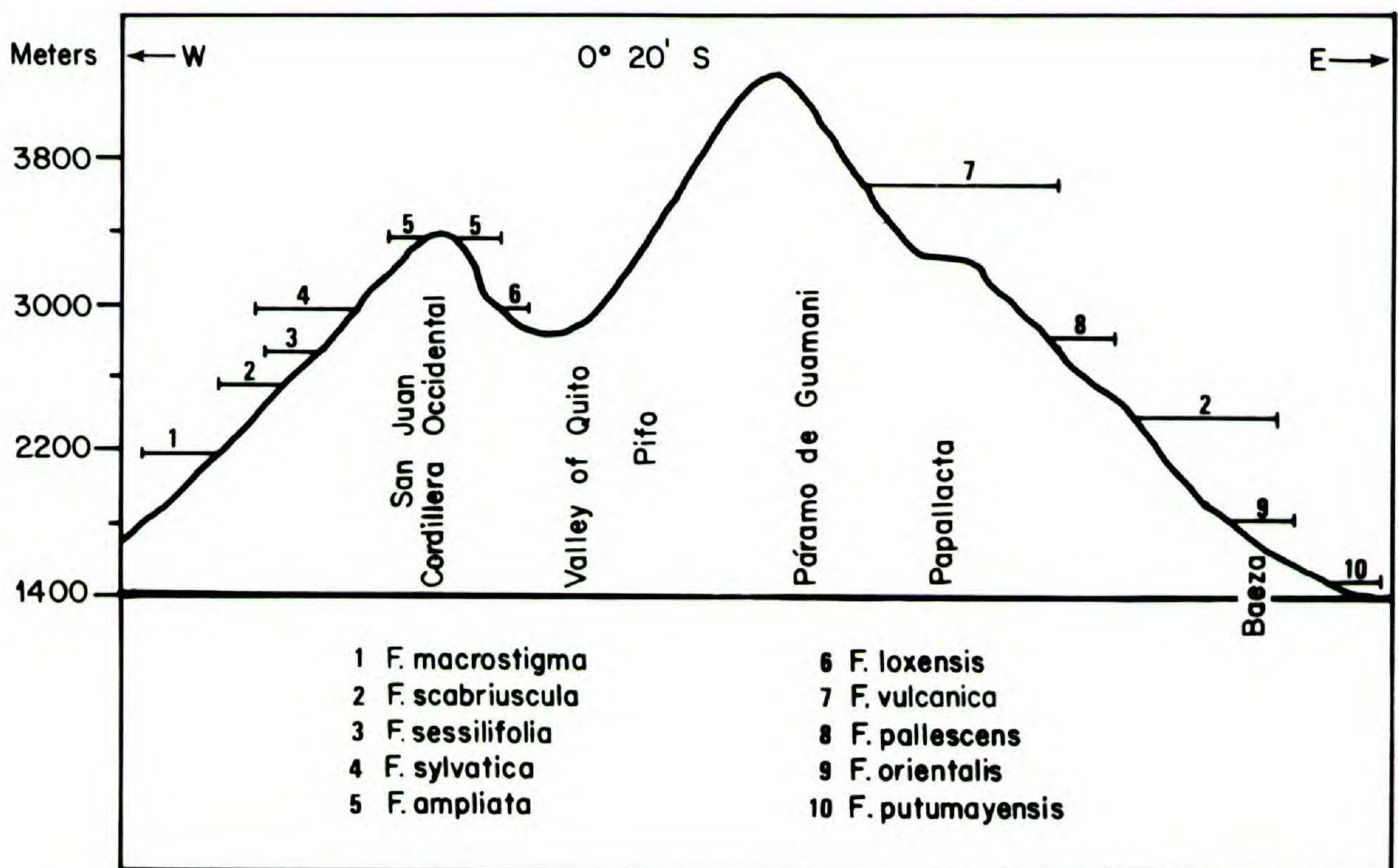


FIGURE 9. Altitudinal zonation of *Fuchsia* along a transect crossing the Ecuadorian Andes in Prov. Pichincha and Napo.

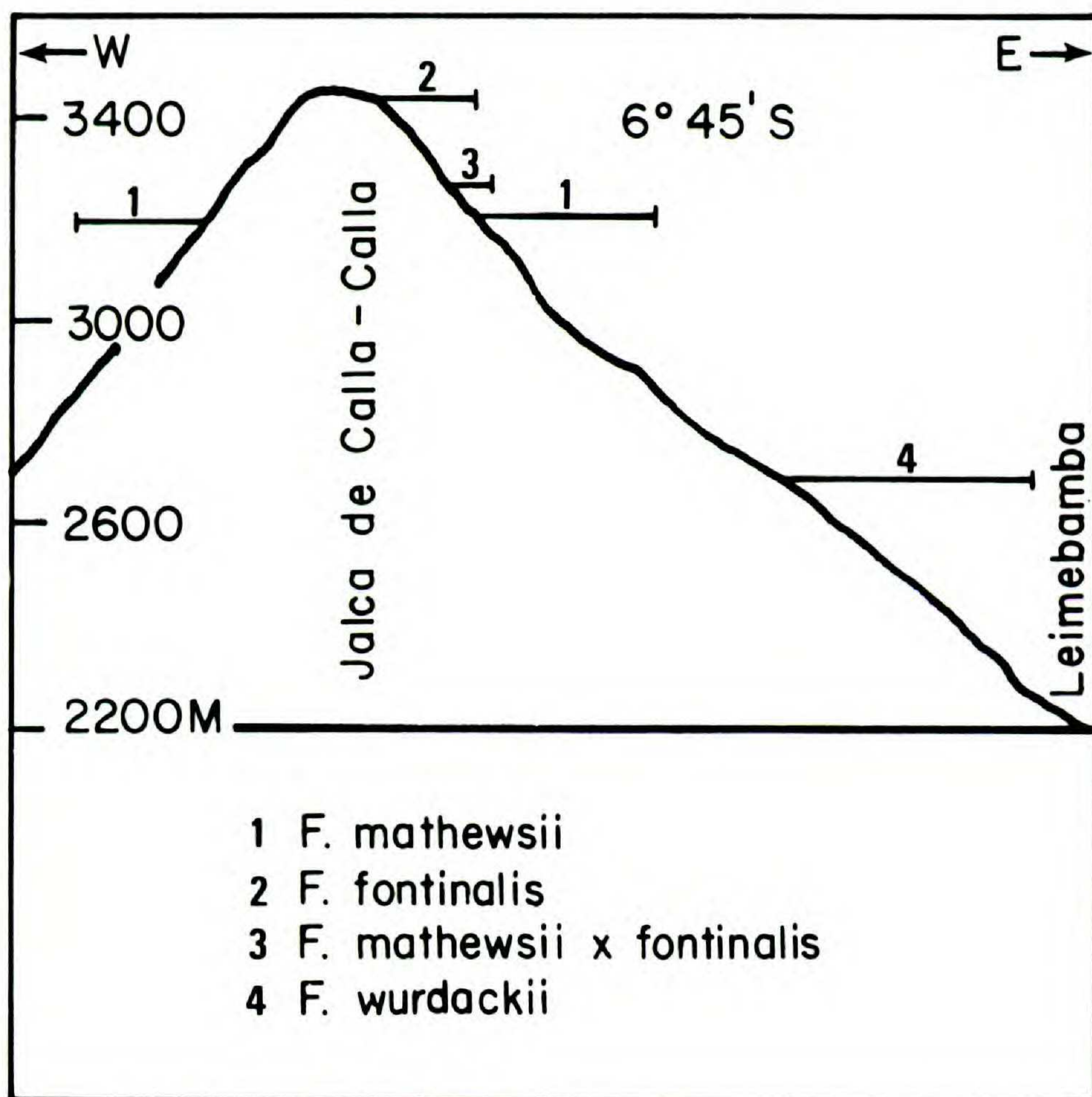


FIGURE 10. Altitudinal zonation of *Fuchsia* along a transect crossing the Cerro de Calla-Calla, Dept. Amazonas, Peru.

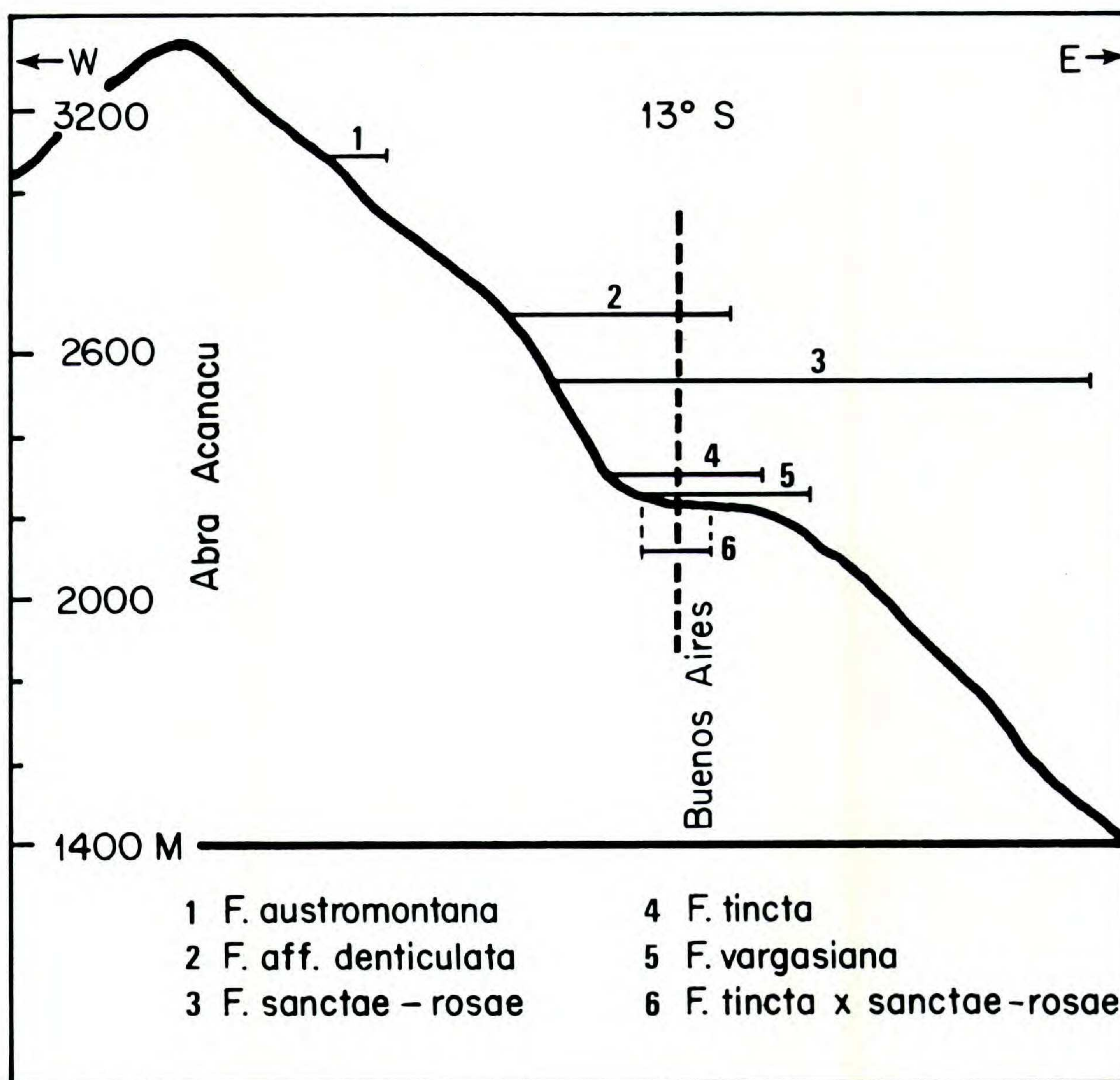


FIGURE 11. Altitudinal zonation of *Fuchsia* along a transect on the eastern slopes of the Peruvian Andes in Dept. Cuzco, Prov. Paucartambo. The vertical dashed line indicates the high degree of sympatry in the vicinity of Buenos Aires.

have been detected on high peaks of the tropical Andes, and detailed palynological evidence from the northern Andes (Hammen, 1974) shows that a maximum temperature depression of 7°C and a lowering of the upper elevation vegetation zones by 1,200–1,500 m occurred during recent glacials (Fig. 13). Glacial episodes were often accompanied by much drier periods than at present. The implications of these climatic fluctuations are complex and different for plants of different altitudes and humidity regimes. For instance, páramo organisms, as well as those adapted to dry, lowland habitats, experienced periods of range extension and secondary contact during the glacials. Moist lowland taxa, on the other hand, underwent isolation and differentiation during glacial episodes. During interglacials such as at present, the dry lowland and high páramo organisms became restricted to island-like enclaves.

The preceding events regarding the recent history of the Andes have several important biogeographical and evolutionary implications for sect. *Fuchsia*. First, assuming that the ancestors of sect. *Fuchsia* were adapted to cool temperate

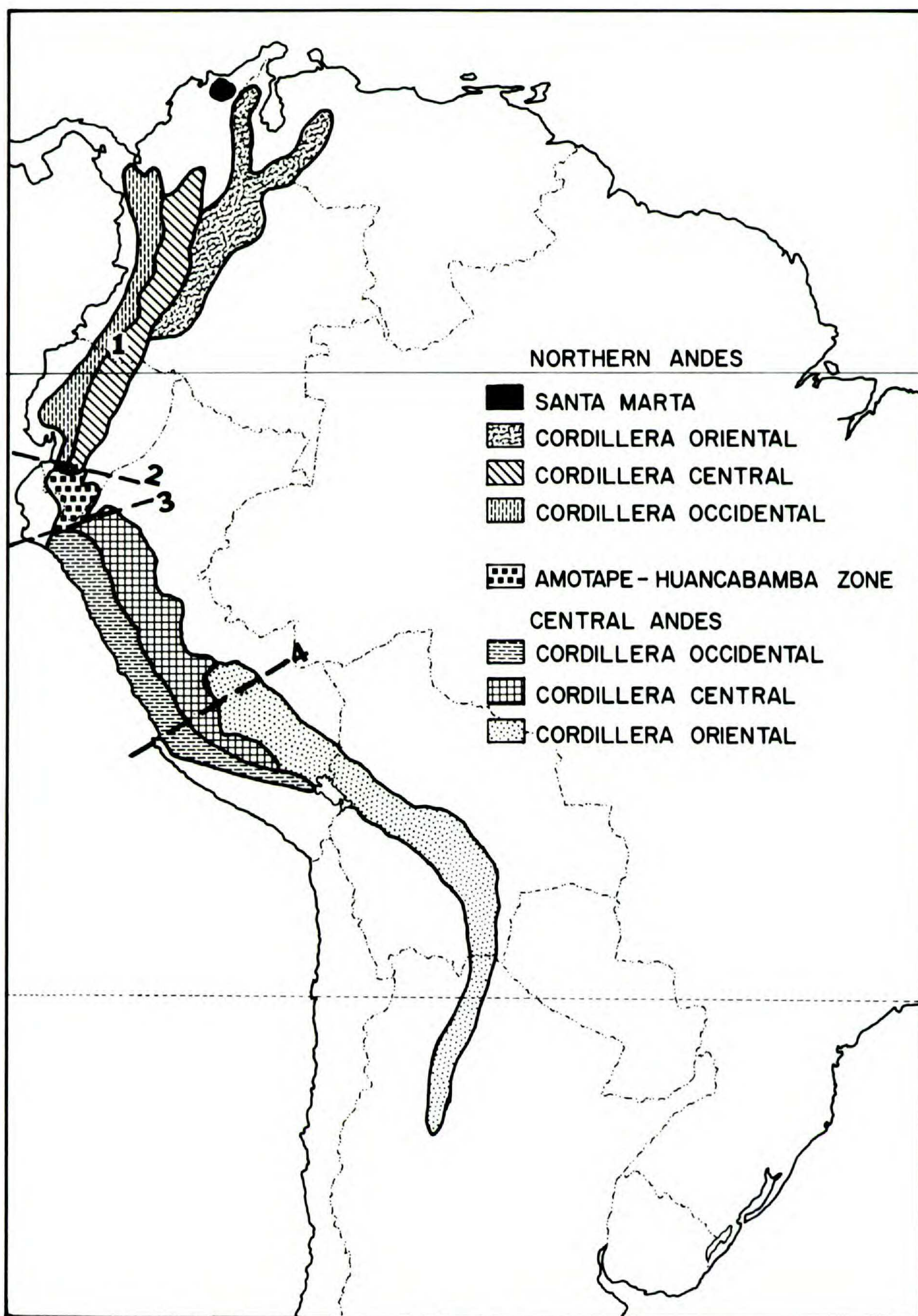


FIGURE 12. Major structural units of the Andes where *Fuchsia* sect. *Fuchsia* occurs. Adapted from Simpson (1979) and Sillitoe (1974). 1 = Nudo de Pasto. 2 = Amotape zone, the northern limit of the Central Andes and a major tectonic segment boundary, aligned to the west with the Carnegie Ridge and the Gulf of Guayaquil. To the north a marked change in the geology of the Andes occurs, with a line of recent stratovolcanos. 3 = Huancabamba deflection. 4 = Pisco or Abancay deflection, marked by a major step in the coastline, a shallowing of the Peru-Chile trench, and the offshore Nazca Ridge.

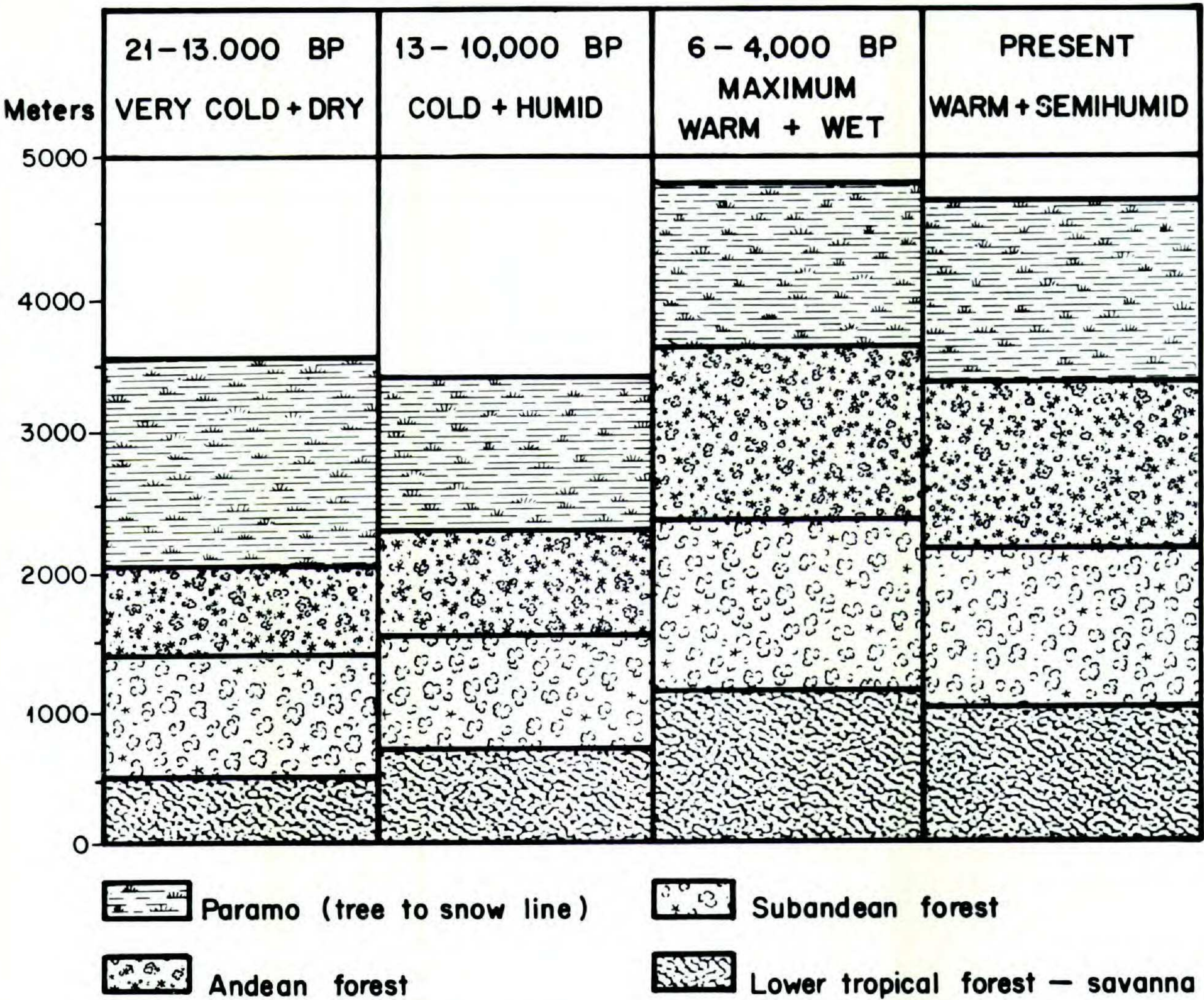


FIGURE 13. Effects of recent climatic fluctuations upon the vegetation zones in the Cordillera Oriental of Colombia. Adapted from Hammen (1974) and Lauer (1979).

habitats as are almost all the extant species in the genus, they could not have arrived in the tropical Andes until the Miocene, and major opportunities for the colonization of Andean forest habitats probably did not arise until the early Pliocene. Second, the glacial periods of the Pleistocene were probably times of range extension and secondary contact for populations of *Fuchsia* that would be comparatively isolated at interglacials such as at present. Though the drier climatic conditions of most glacials would negatively affect mesic groups such as *Fuchsia*, the considerable lowering of the montane vegetation zones (up to 1,500 m lower for Andean forest in the coldest glacials) would cause a great increase in its horizontal distribution, making possible migration and secondary contact of taxa across areas presently occupied by lowland vegetation. Third, a comparison of the species compositions of the different Andean structural units where *Fuchsia* sect. *Fuchsia* occurs should enable us to analyze the nature and directions of some of the migrations that have taken place in the section.

Patterns of distribution. *Fuchsia* is a common element of the cloud forest belt that extends along the eastern slopes of the Andes from northern Colombia and Venezuela to northern Argentina and along the west side of the Andes from Venezuela to northern Peru. The geology and physiognomy of the different struc-

tural units of the Andes have been summarized by Simpson (1975b) and Duellman (1979). The structural units where *Fuchsia* sect. *Fuchsia* occurs are shown in Figure 12. Two basic changes from Simpson's (1975b and 1979) system are introduced, however. First, a small unit called the Amotape-Huancabamba zone is added because both the Amotape zone in southern Ecuador (as treated in Sillitoe, 1974) and the Huancabamba deflection in northern Peru constitute clearly defined tectonic boundaries where major changes in the overall geology of the Andes occur (Sillitoe, 1974). It is therefore misleading to extend the structural units of the Northern Andes south of the Amotape zone to the Huancabamba deflection or to extend those of the Central Andes north of the Huancabamba deflection into Ecuador. Though several authors considered the Huancabamba deflection to be the main north-south migration barrier in Andean organisms (Vuilleumier, 1971; Simpson 1975b, 1979; Duellman, 1979), this is least true for cloud forest organisms. The 21 species of amphibians and reptiles that occur both north and south of the Huancabamba deflection are primarily cloud or wet forest inhabitants on the eastern slopes of the Andes (Duellman, 1979). In sect. *Fuchsia* and perhaps in other cloud forest organisms, it is perhaps more appropriate to treat the entire Amotape-Huancabamba zone as the transitional area between the species of the Northern and Central Andes.

The second change is the separation of Simpson's (1975b, 1979) "Cordillera Oriental" of the Central Andes into two units, the Cordillera Central to the north and the Cordillera Oriental to the southeast. This aids our analysis of species distributions by producing three units in the Central Andes that are comparable in size and extent to the units of the Northern Andes. Tectonically and geologically, however, there are ample reasons for this division as well. The dividing line of the two units corresponds to the Pisco or Abancay deflection (Fig. 12), which is marked on the western side by the offshore Nazca ridge, a major step in the coastline, and a shallowing of the offshore Peru-Chile trench. Along the boundary in the mountains to the east, there is a marked northward narrowing of the cordilleras, a change in direction of the Eastern Cordillera, and important changes in the Mesozoic paleogeography (Sillitoe, 1974).

Figure 14 summarizes the species and species group distributions in the different structural units of the Andes where sect. *Fuchsia* occurs. The following discussion deals with the species relationships of each unit. Reference is also made to species distribution maps (Figs. 55-67) in order to explain patterns observed within and between the structural units.

Northern Andes

Sierra Nevada de Santa Marta. This is a small, isolated volcanic range and the northernmost segment of the Andes. It has undergone a complex geological history, but the Sierra Nevada de Santa Marta was underwater until the Miocene and apparently experienced its major upheaval in the Quaternary (Simpson, 1975b). The sole species of sect. *Fuchsia* that occurs there is *F. magdalенаe*, which is endemic to the Andean forest and subpáramo of this small, but high, mountain massif. General floral characters place this species closest to the Peruvian-centered *F. denticulata* species group, but it is very unusual in the section because

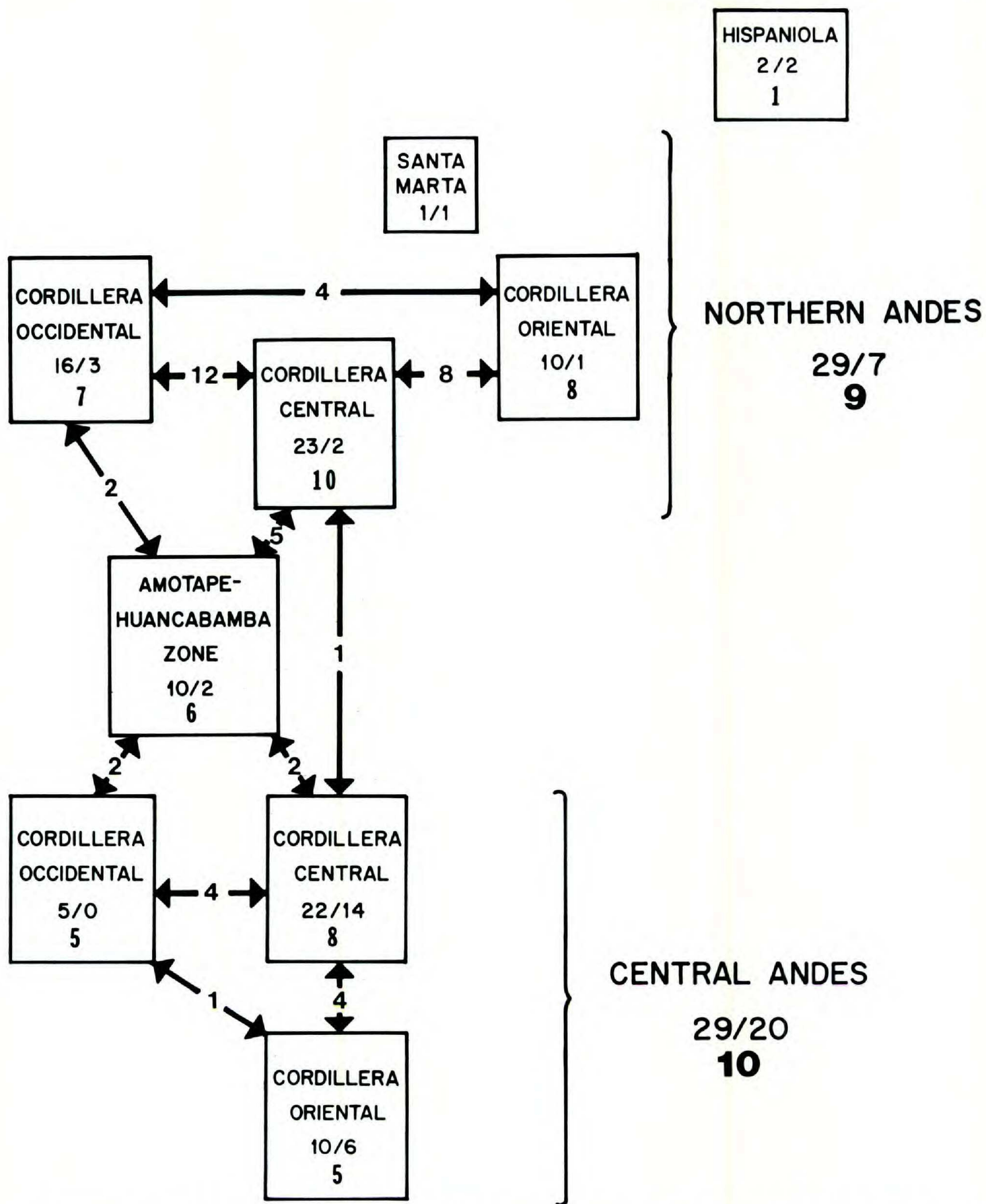


FIGURE 14. Schematic representation of the species composition of *Fuchsia* sect. *Fuchsia* in the major structural units of the Andes (see also Fig. 12). The first number of each pair separated by a slash is the total number of species in that unit; the second number is the number of species found only in that unit (= endemics). The bold face number below each of the above pairs is the number of species groups present in that unit. Numbers of species shared by two units appear between the arrows connecting different units.

of its tetraploidy with biporate pollen and its smooth, non-annular nectaries. Although suitable habitats for *Fuchsia* are found less than 40 km away across the Cesar depression in the Sierra de Perijá of the Cordillera Oriental, the only species of the genus that occurs there is *F. gehrigeri*, which bears no close

relationship to *F. magdalenae* and is found elsewhere only in the Mérida Andes of Venezuela. Mayr (1963) has noted that peripheral isolates of many genera show one or more of the following characters: they usually occur in a small geographical area, have low absolute population sizes, and differ from the main body of the species in several, often unique morphological or other characters, criteria that apply well to *F. magdalenae*.

Cordillera Oriental. This unit is characterized by a comparatively low number of species but a high number of species groups, low endemism, and strong east-west and north-south connections to neighboring cordilleras.

As shown by van der Hammen's detailed geological and palynological studies of the Cordillera Oriental of Colombia (Hammen, 1974) this unit was uplifted to nearly its present level in the mid- to late Pliocene, followed by a long sequence of glacials and interglacials during the Pleistocene. Through the examination of lacustrine sediments, van der Hammen and coworkers were able to document recent climatic extremes. During the Last Glacial, at 21,000 years BP, the climate around the high plains of Bogotá became extremely cold and dry, with a ca. 7°C temperature depression and a 1,200–1,500 m vegetation zone lowering compared to the present. In the Middle Holocene, a "hypsothermal" occurred in the current interglacial when the temperature became 2°C warmer and the vegetation zones several hundred m higher than at present. The average effects of these climatic changes on the altitudinal distribution of different vegetation zones are illustrated in Figure 13.

Considering the magnitude of the vegetation zone fluctuations during the Pleistocene, migrations of *Fuchsia* across the Magdalena and Cauca River valleys to the Cordilleras Central and Occidental could have occurred almost without interruption or via bird dispersal across short lowland barriers. At present, there is only a 35 km gap between the 1,000 m contours of the Cordillera Central and the Cordillera Oriental at 5°N Latitude, which is the approximate latitude of Bogotá and where *F. hirtella*, *F. petiolaris*, and *F. venusta* are found in both cordilleras. These species are all more common in the Cordillera Oriental than in the Cordillera Central, and they most likely migrated in a westerly direction to attain their present distribution there. The distribution patterns of the large páramo genera *Espeletia* and *Puya* give strong evidence of the same pattern of a Cordillera Oriental source area with subsequent migrations to the Cordillera Central (Cuatrecasas, 1979). The recent origin of these páramo genera (Hammen, 1979) further supports the idea that the Pleistocene was an important period for plant migrations in the Andes.

In its southern extreme, the Cordillera Oriental abuts the Cordillera Central just north of the Nudo de Pasto. Also known as the Macizo Colombiano, the Nudo de Pasto (Fig. 12) is a high massif in southern Colombia and northernmost Ecuador that has acted as a very effective migration corridor for Andean species that spread into the three different units that diverge northwards from it. Several species of *Fuchsia* have present day distributions that indicate they used this corridor to reach the southern part of the Cordillera Oriental from the south. These include *Fuchsia sessilifolia* (Fig. 63), *F. scabriuscula* (Fig. 56), and *F. cuatrecasasii* (Fig. 58). The first of these species probably used the Nudo de

Pasto as a corridor to spread northwards into all three units of the Northern Andes. *Fuchsia verrucosa* (Fig. 65), which is centered in the Cordillera Oriental, has a distribution indicating that it migrated southwards along the eastern edge of the Nudo de Pasto to reach its present locations in the Cordillera Central in southern Colombia.

In the north, the Cordillera Oriental splits into two ranges near the Colombian-Venezuelan border, the Sierra de Perijá to the north, and the Mérida Andes to the northeast. The Mérida Andes are separated from the Colombian Andes by the low Táchira depression, which constitutes a secondary dispersal barrier within this unit. Six species occur just on the Colombian side of the barrier, and the only endemic species in this unit, *F. gehrigeri*, is found only in the Mérida Andes and the Sierra de Perijá.

In summary, the distribution patterns of this unit show close ties to the adjacent Cordillera Central, with all but one species and numerous species groups shared between them. The presence of so many species in common and their relative lack of differentiation in the different cordilleras suggests that they have not been separated for very long or that they have been in secondary contact, and it is shown how Pleistocene climatic changes could easily account for migrations or secondary contact of species between the two cordilleras.

Cordillera Central. This unit has the highest representation of species and species groups, yet the next lowest proportion of endemism of any structural unit. This is largely due to the central position of this unit in the Northern Andes and its close proximity to three adjacent units. The more gently sloping eastern flanks of the Cordillera Central offers a greater variety of habitats than the comparatively steep slopes of the Cordillera Occidental.

Twelve species are common to both the Cordillera Central and the Cordillera Occidental. The high interandean valleys of Ecuador, the Nudo de Pasco, and the high plateau separating the Cauca and Patía Rivers are major corridors for species exchange between these two units, and they all must have greatly facilitated migration of upper montane species during Pleistocene glacials.

The *Fuchsia petiolaris* species group, which is strongly centered in the Cordillera Central, has complex patterns of variability between populations and is the source of considerable taxonomic confusion. In Ecuador, populations of this species group are found on many of the high, semi-isolated peaks that are found in both cordilleras (Fig. 59). Since members of this group typically occur at high elevations near tree line, they were probably more strongly affected by Pleistocene events than other groups in the section; Sauer (1971) recorded three main glaciations in Ecuador. The *F. dependens* species group also developed strongly in a relatively small area centered in the Cordillera Central in southern Colombia (Fig. 66).

Cordillera Occidental. Seventy-five percent of the species in this unit are shared with the Cordillera Central, while only three species are endemic there. *Fuchsia sylvatica* occurs on the Pacific slopes in Ecuador and is vicarious with *F. nigricans*, which is found in the same cordillera but north of the Patía River valley in southern Colombia. *Fuchsia macrostigma*, however, occurs on both sides of the Patía River, which is a secondary migration barrier within this unit. Two of the

endemic species, *F. cinerea* and *F. polyantha*, are very localized and occur on the edge of the Nudo de Pasto.

Amotape-Huancabamba Zone

Despite its relatively small area (Fig. 12), this unit has the same number of species as the much larger Cordillera Oriental of the Northern Andes. This reflects its key position bordering four different structural units, as well as the equatorially based center of species diversity in the section. *Fuchsia glaberrima* is the only species that occurs both north and south of this unit. The Amotape-Huancabamba Zone thus constitutes the major transitional zone between the species of the Northern and Central Andes. The species found within this unit, however, are a mixture from all four adjacent structural units and include two endemic species. This area is still insufficiently collected because of its inaccessibility, and future explorations will be certain of finding novelties in *Fuchsia*. One of the most distinctive species in the section, *F. steyermarkii*, occurs there and appears to be most closely allied to species from the Cordillera Central in northern Peru.

Central Andes

Cordillera Occidental. The cloud forest belt on the western side of the Andes ends near the Peruvian-Ecuadorian border. As a result, most of the Cordillera Occidental in Peru is too dry for *Fuchsia*, and four of the five species present in this unit are only found north of 8°S Latitude. These species inhabit local patches of mesic forest that is more a mixed scrub than true cloud forest. *Fuchsia ayavacensis* is the only species that is largely restricted to this unit, and it forms part of the northern *F. petiolaris* species group. Three of the species in the unit are shared with the Cordillera Central of Peru and probably were dispersed across the Marañón River valley from the east. At present, there are only approximately 25 km separating the closest populations of *F. mathewsii* on either side of the Río Marañón. The genus *Ascidogyne* (Compositae) provides another interesting example of this trans-Marañón disjunction (Cuatrecasas, 1979). This unique genus has only two species, one in the high "jalca" of Dept. Amazonas in northern Peru, and the other across the Marañón valley to the west in Dept. Cajamarca.

Fuchsia denticulata is an exceptional species in this unit because it is found between 9°S and 13°S Latitude in isolated pockets of mesic vegetation on the otherwise arid Pacific slopes of Depts. Lima and Ancash. This species is widespread on the eastern slopes of the Andes, however, from Dept. Huánuco in Peru to Dept. Cochabamba in Bolivia. This disjunct pattern was previously discussed by Simpson (1975b, 1979) for other mesic Andean species. Simpson (1975a) postulated that the high parts of the Cordillera Occidental and its upper western slopes experienced heavier precipitation during Pleistocene glacial periods than at present. At these times, east-west migrations of mesic montane plant taxa were made possible across the "nudos" or low connecting paths between the Pacific and Amazonian slopes of the Peruvian Andes. *Fuchsia denticulata* is a clear example of migration directly across the Andes via the Nudo de Pasco, at the

latitude of Lima. There are fewer than 100 km (air distance) now separating the closest populations of *F. denticulata* on the western slopes above Lima and on the eastern slopes in Dept. Junín (Fig. 61). Besides its presence in cloud forests of the Cordillera Central in Junín, *F. denticulata* also occurs in higher interandean valleys such as the valley of Comas, which has an intermediate habitat type between the eastern “ceja” and the small mesic pockets restricted to protected canyons on the western slopes. This distribution pattern suggests how species with wide ecological tolerances may have been able to cross the Nudo de Pasco under more humid conditions than exist at present. Once *F. denticulata* reached the Pacific slopes, it probably spread north (and south?) in what may have been a continuous moist forest belt during Pleistocene glacials (Simpson, 1975a, 1979). Other species such as *Arracacia incisa* Wolff. (Umbelliferae) show the same pattern as *F. denticulata*, and Simpson (1975b) gave several examples of species that are presently disjunct between the western slopes above Lima and the eastern slopes further south near Cuzco. These latter species may have used a more southern pass, the Nudo de Vilcanota.

Cordillera Central. This unit has almost as high a species diversity as the Cordillera Central of the Northern Andes, but two fewer species groups and a much higher proportion of endemic species. It is much more dissected and is in contact with fewer units than the northern Cordillera Central. The adjacent Cordillera Occidental is too dry to allow major opportunities for the establishment of new populations of *Fuchsia*, and strong migratory barriers are present to the north in the Huancabamba depression and to the south in the Río Apurímac valley. Though there are proportionately fewer species groups present in this unit than in most others, at least half of those groups present are restricted or strongly centered here. All four species of the *F. simplicicaulis* species groups are endemic to the Cordillera Central, as are all but one species each of the *F. macrophylla*, *F. boliviana*, and *F. decussata* species groups. Speciation has probably been facilitated by the presence of several semi-isolated ranges such as the Cordillera Azul on the Huánuco-Loreto border. Five very localized endemics are concentrated in Dept. Amazonas of northern Peru.

Cordillera Oriental. As in the Cordillera Oriental of the northern Andes, ten species of *Fuchsia* occur in this unit, but a lower number of species groups and a much higher proportion of endemic species are found here. The Cordillera Oriental of Peru and Bolivia is more isolated from other units where sect. *Fuchsia* occurs than the northern cordilleras. Four species, *F. boliviana*, *F. austromontana*, *F. denticulata*, and *F. sanctae-rosae*, occur from southern Peru into Bolivia, showing the continuity of distribution of most species in this unit across the outer slopes of the Titicaca Basin. *Fuchsia boliviana* just barely extends north of the Río Apurímac into the Cordillera Central, and it may only be naturalized there. *Fuchsia tinctoria* and *F. vargasiana* are restricted to one or two valleys in southern Peru, but are very closely related to the Bolivian *F. furfuracea*. *Fuchsia macrophylla* and *F. decussata* are both centered in the Cordillera Central and just enter the northern part of the Cordillera Oriental. The only species group of this unit that reaches the northern Andes is the *F. denticulata* group.

Hispaniola

Two species of sect. *Fuchsia* are widely disjunct from the rest of the species in the section and are endemic to the Caribbean island of Hispaniola. A similar Andean-Hispaniola disjunction of montane species has recently been reported by Cuatrecasas (1979) for the genus *Laestadia* (Compositae), which has four species in the Andean páramos, one in high elevation Costa Rica, and one on Hispaniola. The ancestors of the fuchsias on Hispaniola probably reached the island from South America by long distance bird dispersal, a mechanism that has been proposed to account for other disjunctions in the genus, such as *F. cyrtandroides* on Tahiti. Judging from the lack of clear affinities of either of the two Hispaniola species to any species group on the South American mainland, their arrival to the island does not appear to be recent. It is furthermore unclear whether *F. triphylla* and *F. pringsheimii* were derived from a common ancestor or whether they arrived separately, by a "double invasion" in the sense of Mayr (1963). Supporting the possibility of a common ancestor, both species have the combination of tetraploidy with biporate pollen, which is unusual in the genus. In addition, they are presently isolated altitudinally throughout their range, except in certain contact areas where partly fertile hybrids are formed. On the other hand, the two species differ widely in morphological characters (Table 19). *Fuchsia triphylla* is morphologically similar to the main body of Andean species of sect. *Fuchsia*, but *F. pringsheimii* has several floral characters not clearly related to any section in the genus, such as particular non-annular nectaries and very large, emarginate petals. If a double invasion did occur, then *F. pringsheimii* is most likely the descendant of the earlier immigrant, and its unique assemblage of characters may even be derived from the early offshoot of the genus that had reached Central America.

Summary of Distribution Patterns

A small number of taxa in *Fuchsia* sect. *Fuchsia* show wide disjunctions in range from the main body of species in the Andes or from other members of their species groups. These include species such as *F. magdalenae* in the Sierra Nevada de Santa Marta and *F. triphylla* and *F. pringsheimii* on Hispaniola. These species show fundamental differences from each other and from the main body of the section in several morphological and cytological features. In this way, they can be considered peripheral isolates in the sense of Mayr (1963) and may represent early offshoots of the section that were isolated at the margins of the range.

In the contiguous structural units of the Andes where the bulk of the species in sect. *Fuchsia* are concentrated, a major change in the species and species group composition occurs in southern Ecuador and northern Peru in a transitional area called the Amotape-Huancabamba zone. Only one species and four species groups occur both north and south of this area. Consequently, it has been possible to compare the distribution patterns of the species in the Northern Andes with those of the Central Andes.

As seen in Figure 14, the Northern and Central Andes each have 29 species and nearly the same number of species groups. The structural units with the greatest number of species are the Cordillera Central of the Northern Andes and

the Cordillera Central of the Central Andes. While we cannot place the center of diversity of the section in either one of these two areas, it is clearly located on the eastern slopes of the Andes in Ecuador and northern Peru. From there, we find a gradual reduction in species number to the north and south in a pattern analogous to the distribution of hummingbird species (Skutch, 1973).

Just over half (32 of 61) of the species in sect. *Fuchsia* are restricted to a single structural unit of the Andes or to the island of Hispaniola. As might be expected of easily dispersed plants in the cloud forest belt, this proportion is lower than that normally observed in páramo plants, where high degrees of local endemism are common (Simpson, 1975b; Cuatrecasas, 1979). The proportion of endemics (= species limited to a single structural unit) in sect. *Fuchsia* varies significantly, however, between the Northern and Central Andes. In the Northern Andes, with 24% endemics, migration between structural units has been facilitated by the proximity of the three cordilleras and the numerous corridors that would be available in glacial periods of lowered vegetation zones. Accordingly, four species in the Northern Andes are present in all three cordilleras, and twelve are found in two cordilleras. In contrast, the Central Andes have 69% of the species endemic, with only one species present in all three cordilleras and five in two cordilleras. The Central Andes have much stronger migration barriers because of the greater spatial isolation of the Cordilleras Central and Oriental, and the aridity of the Cordillera Occidental.

The key migratory corridor in the Northern Andes has been the Nudo de Pasto (Macizo Colombiano). The three northern cordilleras merge at this massif, and many species have used it to disperse latitudinally or longitudinally into the different structural units. A total of 14 species are present along the Nudo de Pasto (as defined by Duellman, 1979), which is the richest local species concentration of sect. *Fuchsia* in the Andes.

Although the Cordillera Oriental of the Northern Andes is poorer in species number than the adjacent Cordillera Central, it has been an important source area of several species present in the northern part of the Cordilleras Central and Occidental. At least three species have migrated westwards across the Magdalena valley, and one or two migrated further west across the Cauca valley into the Cordillera Occidental. In Ecuador, the opportunities for migration between the two cordilleras have been numerous, and it is difficult to determine for most species in which direction they may have spread.

Most species groups of the Central Andes are restricted to a single structural unit, but three migration paths between different structural units were identified, 1) the western migration of two or three species across the Marañón River in northern Peru, 2) the western migration of *Fuchsia denticulata* across the Andes to the Pacific slopes via the Nudo de Pasco, and 3) the southern expansion of two species from the Cordillera Central into the Cordillera Oriental.

Secondary barriers exist within many structural units that have also been important filters to migration. For example, only three of ten species in the Cordillera Oriental of the Northern Andes occur on both sides of the Táchira depression in western Venezuela. Similarly, the Patía River valley in southwestern Colombia and the Huallaga and Mantaro Rivers in central Peru have also acted as selective barriers within their respective units.

REPRODUCTIVE BIOLOGY

FLORAL BIOLOGY

The maturation sequence of flowers seems to be similar in all species of sect. *Fuchsia*. Anthesis usually occurs in the early morning, at which time the stigmatic surface becomes wet with a sticky exudate and is presumably receptive (Raven, 1979a). Anther dehiscence is usually delayed from several hours to one or two days, depending on the species, but the stigma remains receptive in all species until after the anthers open; protogyny is ubiquitous but does not preclude self-pollination. Flowers last an average of three to four days from anthesis to abscission. A spatial separation of 2–20 mm usually exists between the stamens and the exerted stigma, further reinforcing outcrossing. Notable exceptions, however, are *F. boliviana*, *F. nigricans*, and *F. verrucosa*, in which at least some populations have the stigma in close contact with the upper staminal whorl. In other species, if no pollinator visits are made before anther dehiscence, the stigma-anther separation is usually small enough that wind or other mechanical factors are sufficient to cause self-pollination. Self-pollination is favored because the pollen is held together in elastic strings by their viscin threads and because the stigma is situated below the anthers in the hanging flowers that characterize sect. *Fuchsia*.

As far as known, all species of *Fuchsia* are self-compatible, which is considered an advanced character state in the family (Raven, 1979a). *Fuchsia* is the only genus in the family in which marked protogyny occurs. Although Raven (1979a, p. 578) reports protogyny in *Circaea*, it is barely pronounced and therefore not really comparable to the protogyny found in certain sections of *Fuchsia*.

Controlled crosses in both native and naturalized populations of *F. boliviana* show that this species is self-compatible and largely autogamous. The high degree of autogamy is probably exceptional in the section and undoubtedly helps to account for the widely naturalized distribution of *F. boliviana* at present. In this species, protogyny is very poorly developed, and the anthers and stigma are in close contact; naturalized populations at El Junquito, Venezuela, were found to self-pollinate in bud.

Male sterility is an outcrossing device that is found in the Onagraceae only in certain sections of the genus *Fuchsia*. All the known sections with male sterility are small and have distributions that are peripheral to the main Andean-Brazilian center of the genus. One possible case of gynodioecy has now been found in sect. *Fuchsia*, however. Certain populations of *F. hartwegii* from several different localities in Colombia include male-sterile individuals. Other populations of the same species apparently consist entirely of hermaphroditic plants. A similar situation has recently been documented in *F. paniculata* (sect. *Schufia*) of Central America (Breedlove et al., 1982). Further field work and breeding studies are needed to clarify the situation of male sterility in *F. hartwegii*, but its confirmation would constitute the fifth independent occurrence of male sterility in the genus.

POLLINATION

Table 3 shows the features of sect. *Fuchsia* that strongly associate it with hummingbird pollination. In addition, the beaded viscin threads, which enable

TABLE 3. Characters of *Fuchsia* sect. *Fuchsia* adapted to hummingbird pollination.

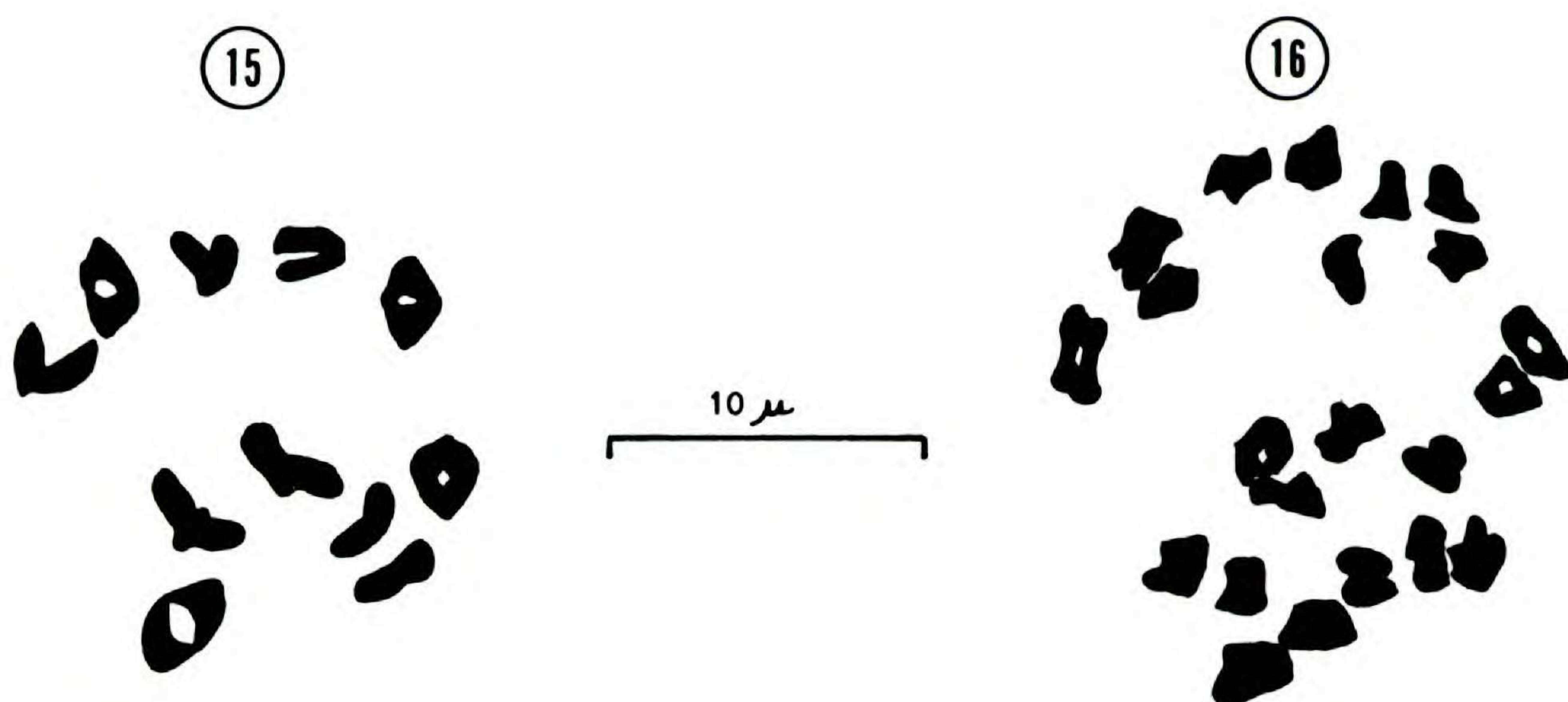
	Hummingbirds ¹	<i>Fuchsia</i> sect. <i>Fuchsia</i>
<i>Distribution:</i>	New World, highest diversity in the tropical Andes.	Tropical Andes, Hispaniola
<i>General behavior/phenology:</i>	Tropical species are non-migratory, territorial, diurnal.	Plants long-lived with diurnal anthesis, long-lived flowers (av. 3–4 days), and long flowering season.
<i>Pollination-related characters:</i>	Poor sense of smell, preference for red coloration, long bill and sucking tongue, hovering approach, high energy requirement, and frequent daily feeding.	Flowers odorless, reddish, tubular, divergent to pendulous, copious nectar production.

¹ From Grant & Grant, 1968; Percival, 1969; Raven, 1972a.

hundreds of grains to be removed in a single bundle, appear to be of adaptive value in bird pollination (Percival, 1969; Skvarla et al., 1978). The hummingbirds feed on the nectar that is produced at the base of the floral tubes, and, unlike many groups of insects, they remain active in the rain and at cool temperatures, an obvious advantage for montane cloud forest groups such as *Fuchsia* (Heinrich & Raven, 1972).

Only incidental observations were made on pollination in *Fuchsia* during the course of field work. Numerous unidentified hummingbird species were seen visiting different species of *Fuchsia* sects. *Fuchsia* and *Hemsleyella*, and no non-avian visitors were observed. On Hispaniola, there are two species of *Fuchsia* that occur at different altitudes and three resident species of hummingbirds. *Chlorostilbon swainsonii*, which is the “large highland species” of Lack’s (1976) niche theory of West Indian hummingbirds, feeds exclusively below the canopy (Lack, 1976) and has been photographed visiting *F. triphylla* (Fig. 32). Lack’s “large lowland species,” *Anthracothonax dominicus*, is actually present in the highlands there, but is restricted to the tree canopies. The third “small species” completing the hummingbird fauna of the island is *Mellisuga minima*, which occurs at all elevations. But because it is the second smallest bird in the world it is therefore very unlikely to pollinate the moderately long-tubed *F. triphylla* and *F. pringsheimii*. The hybrids found between these two species of *Fuchsia* in areas where their altitudinal limits are in close proximity can almost certainly be attributed to visits by *Chlorostilbon*, which ranges throughout the elevational ranges of both species and occupies the understory niche almost exclusively.

Naturalized populations of *F. boliviana* were observed over a several day period in March 1979, at El Junquito and Colonia Tovar, Venezuela. Two different populations were aggressively defended and visited throughout the day by the long tailed sylph, *Agelaiocercus kingi*. None of the visits were legitimate pollinations, however, because the hummingbird consistently pierced the base of the tube and robbed the flowers of their nectar. At higher elevations in the Colonia Tovar, the same species of *Fuchsia* was visited by the booted racket-tail, *Ocreatus underwoodii*, which appeared to be making legitimate visits without piercing the tube.



FIGURES 15–16. Meiotic chromosomes in *Fuchsia* sect. *Fuchsia*, metaphase I.—15. *F. loxensis*, $n = 11$, from Berry 3133 (MO).—16. *F. verrucosa*, a tetraploid, $n = 22$, from Berry 3662 (MO).

In several cases two closely related species differ mainly in floral tube length and coloration, yet occur together or in close proximity without the presence of intermediate plants. *Fuchsia polyantha*, which has red flowers 34–43 mm long, grows with *F. sessilifolia*, which has pale pink tubes 13–20 mm long. A similar pattern is found between *F. tinctoria* and *F. vargasiana*, and between *F. macrophylla* and *F. macropetala*. This pattern suggests that hummingbird species are species-specific pollinators of *Fuchsia*, the specificity linked to tube lengths and color patterns, or that flower dimensions mechanically act against interspecific pollination. In hawkmoth-pollinated species of *Oenothera*, Gregory (1964) found that short-tubed flowers were only effectively pollinated by short-tongued hawkmoths, but long-tubed species were able to use long-tongued as well as short-tongued hawkmoths as effective pollinators.

Further observations on the pollination system of sect. *Fuchsia* are needed and could analyze specific problems such as the degree of specificity between hummingbirds and *Fuchsia* species, the relation of bill length to tube length, the importance of territoriality of hummingbirds in pollen dispersal, and the possible presence of insect pollinators.

VEGETATIVE REPRODUCTION

Trailing stems or broken stem pieces of *Fuchsia* root readily in the moist humus that is usually found in thickets where most species of the genus occur. Large colonies of *F. boliviana* that reproduce mainly in this manner were seen in Venezuela (naturalized) and in Bolivia (native). The same process also gives rise in other species to dense thickets of plants that probably arose from a single individual. In 1979 I returned to the precise locality of a hybrid between *F. gehrigeri* and *F. nigricans* that had first been collected in 1958 and found what was most probably the same population. Regrowth from viable hybrid seed cannot be discounted, but the uniformity of the population and the large number of vigorous, young shoots make it more likely that vegetative reproduction has maintained this colony for over 20 years.

DISPERSAL

Fuchsia is the only genus of Onagraceae with fleshy fruits, clearly an advanced character within the family. The berries are plump and generally reddish at maturity, with a high sugar content, and are clearly adapted to dispersal by birds.

Berries are well suited for long distance dispersal, and the distribution of widely disjunct species such as *F. cyrtandroides* on Tahiti and *F. triphylla* on Hispaniola have been explained by internal transport by birds (Carlquist, 1967). A similar long-distance dispersal event has been postulated for the early establishment of the Mexican and Central American sections of the genus. On a local scale, bird dispersal is an effective means of spreading seeds to new habitats, and it probably has been instrumental in the extension of many species into different structural units of the Andes.

CYTOLOGY

Compared with those of other Onagraceae, the chromosomes of *Fuchsia* are relatively large and unspecialized, contract evenly in the course of mitosis, and show poor differentiation into heterochromatic and euchromatic portions (Kurabayashi et al., 1962). Translocation systems common in the tribe Onagreae and aneuploidy prevalent in Lopezieae and in *Clarkia* are not found in *Fuchsia*, which retains the basic chromosome number of the family, $x = 11$.

Reports of chromosome numbers in the native species of *Fuchsia* previous to the beginning of the present study in 1977 were mostly diploid ($n = 11$), except for two tetraploid species in sect. *Quelus*, *Fuchsia lycioides* (sect. *Kierschlegeria*), and a single individual of sect. *Encliandra* (Warth, 1925; Haque, 1952; Chaudhuri, 1956; Beuzenberg & Hair, 1959; Kurabayashi et al., 1962; Huynh, 1965; Breedlove, 1969). The chromosome numbers of only three of the 61 species now recognized in sect. *Fuchsia* had been reported, all diploid, but since vouchers apparently were not preserved, these reports are of little value. Recent studies conducted at the Missouri Botanical Garden have shown sect. *Quelus* (eight spp., Brazil and the southern Andes) to be polyploid, with three tetraploid and one octoploid species known; tetraploid species have been found in the Andean sect. *Hemsleyella* (P. Berry and T. P. Ramamoorthy, unpublished). Because these sections are considered to be rather closely related to sect. *Fuchsia*, an extensive survey was undertaken in sect. *Fuchsia* to determine if polyploidy had played any significant role in the broad diversification of this section.

Methods. Gametic counts were obtained from pollen mother cells in young, field collected buds fixed in 3 parts absolute ethanol : 1 part glacial acetic acid for 24 hours; buds were then transferred to 70% ethanol. Anthers were squashed and stained in aceto-carmin or in lacto-propionic orcein. Somatic chromosome counts were obtained from actively growing root tips pretreated for 2–4 hours in 8-hydroxyquinoline, then fixed as above in acetic alcohol for 10 min. to 6 hr. The roots were hydrolyzed in 1 N HCl for 20 min. at 60°C and stained for 12–24 hr. in aceto-carmin or lacto-propionic orcein; they were then squashed and heated in equal parts glycerine and 45% acetic acid.

Results. One hundred new counts were obtained for populations of *Fuchsia*

TABLE 4. Chromosome numbers in *Fuchsia* sect. *Fuchsia*.¹

Taxon	<i>n</i>	<i>2n</i>	Collection Data or Reference
<i>F. abrupta</i> I. M. Johnston	11		PERU, JUNÍN: 58 km E of Satipo, <i>B3078</i> (MO)
	11		PERU, HUÁNUCO: above Chinchao, <i>Mathias & Taylor 4033</i> (RSA) ²
<i>F. ampliata</i> Benth.	11		ECUADOR, IMBABURA: 8 km W of Laguna Cuicocha, <i>B3169</i> (MO)
	11		ECUADOR, PICHINCHA: 9 km W of Chillogallo, <i>B3234</i> (MO)
<i>F. cf. andrei</i> I. M. Johnston	11		PERU, AMAZONAS: 42 km of E of Pedro Ruiz, <i>B3628</i> (MO)
<i>F. austromontana</i> I. M. Johnston	11	22	PERU, CUZCO: 8 km E of Abra de Acanaco, <i>B2594</i> (MO)
	11	22	PERU, CUZCO: 58 km from Ollantaytambo to Quillabamba, <i>B3035</i> (MO)
<i>F. ayavacensis</i> Humboldt, Bonpland & Kunth	11		PERU, PIURA: 35 km E of Canchaque, <i>B3630</i> (MO)
<i>F. boliviana</i> Carrière	11		COLOMBIA, ANTIOQUIA: Alto de Minas, <i>Escobar 1000</i> (MO)
	11		COLOMBIA, TOLIMA: 29 km W of Fresno, <i>B3552</i> (MO)
	11		MEXICO, CHIAPAS: Chamula, <i>Breedlove 8018</i> (DS)
	11		PERU, CUZCO: Urubamba, <i>B2561</i> (MO)
	11		PERU, APURIMAC: Ampuy, <i>Stork, Horton & Vargas 10595</i> (UC) ²
	11		PERU, HUÁNUCO: 5 km SE of Carpish, <i>Stock & Horton 9921</i> (UC) ²
<i>F. canescens</i> Benth.	11		COLOMBIA, CAUCA: 31 km E of Totoró, <i>B3578</i> (MO)
	11		COLOMBIA, CAUCA: 34 km E of Totoró, <i>B3579</i> (MO)
<i>F. caucana</i> P. Berry	11		COLOMBIA, NARIÑO: 24 km E of Pasto, <i>B3252</i> (MO)
<i>F. ceracea</i> P. Berry	11		PERU, HUÁNUCO: 5 km W of Carpish pass, <i>B3081</i> (MO)
<i>F. cinerea</i> P. Berry	11		ECUADOR, CARCHI: Tufiño, <i>B3147</i> (MO)
<i>F. corollata</i> Benth.	22		ECUADOR, CARCHI: ridge between Tulcán and El Carmelo, <i>B3159</i> (MO)
	22		ECUADOR, IMBABURA: Hacienda Curubí, <i>B3173</i> (MO)
	22		ECUADOR, IMBABURA: 11 km SW of Otavalo to Mojan-da, <i>B3175</i> (MO)
	11		COLOMBIA, CAUCA: 11 km E of Totoró, <i>B3575</i> (MO)
	11		COLOMBIA, CAUCA: 4 km W of Gabriel López, <i>B3576</i> (MO)
	22	44	COLOMBIA, CAUCA: 23 km E of Puracé, <i>B3584</i> (MO)
<i>F. corollata</i> × ? <i>caucana</i> (probable hybrid)	22	44	COLOMBIA, CAUCA: 23 km E of Puracé, <i>B3584</i> (MO)
<i>F. corymbiflora</i> Ruiz & Pavón	11		PERU, HUÁNUCO: Carpish, <i>B3082</i> (MO)
<i>F. crassistipula</i> P. Berry	11		COLOMBIA, TOLIMA: 40 km W of Fresno, <i>B3553</i> (MO)
<i>F. denticulata</i> Ruiz & Pavón	11		BOLIVIA, LA PAZ: road to Chulumani, <i>Albert de Escobar 1305</i> (TEX)
	11		PERU, CUZCO: ca. 70 km from Quillabamba to Ollantaytambo, <i>B2573</i> (MO)
	11	22	PERU, CUZCO: 72 km from Quillabamba to Ollantaytambo, <i>B3042</i> (MO)
		22	PERU, CUZCO: ca. 65 km from Quillabamba to Ollantaytambo, <i>B3048</i> (MO)
		22	PERU, AYACUCHO: 41 km E of Tambo, <i>B3050</i> (MO)
<i>F. aff. denticulata</i> Ruiz & Pavón	11		PERU, CUZCO: Km 131 of Cuzco-Paucartambo-Pilcopata road, <i>B2598</i> (MO)

TABLE 4. Continued.

Taxon	<i>n</i>	<i>2n</i>	Collection Data or Reference
<i>F. dependens</i> Hook.	11		COLOMBIA, NARIÑO: 13 km S of Pasto, <i>B3145</i> (PSO)
	11		ECUADOR, CARCHI: 4 km W of El Carmelo, <i>B3164</i> (MO)
<i>F. ferreyrae</i> P. Berry	11		PERU, JUNÍN: 68 km W of Satipo, <i>B3073</i> (MO)
<i>F. fontinalis</i> J. F. Macbr.	11		PERU, AMAZONAS: 62 km from Balsas to Leimebamba, <i>B3608</i> (MO)
<i>F. gehrigeri</i> Munz	11		VENEZUELA, MÉRIDA: 43 km W of El Águila to Piñango, <i>B3138</i> (MO)
	11		VENEZUELA, MÉRIDA: 9 km above Santo Domingo to Apartaderos, <i>B3139</i> (MO)
	11		VENEZUELA, MÉRIDA: Km 19–20 from Apartaderos to Santo Domingo, <i>B3599</i> (MO)
	11		VENEZUELA, TÁCHIRA: 6 km E of Zumbador to Queniquea, <i>B3297</i> (MO)
<i>F. gehrigeri</i> × <i>nigricans</i>	11		VENEZUELA, TRUJILLO: Visún, above Las Mesitas, <i>B3129</i> (MO)
<i>F. gehrigeri</i> × ? <i>venusta</i>	11		VENEZUELA, TÁCHIRA: 3.5 km E of Zumbador, <i>B3414</i> (MO)
<i>F. hartwegii</i> Benth.	c.11		COLOMBIA, PUTUMAYO: W of Sibundoy, <i>B3255</i> (PSO)
	11		COLOMBIA, VALLE: above El Guayabo, Palmira to Taco, <i>B3568</i> (MO)
	11		COLOMBIA, CAUCA: 21 km E of Piendamó, <i>B3572</i> (MO)
<i>F. hirtella</i> Humboldt, Bonpland & Kunth	c.11		COLOMBIA, CUNDINAMARCA: 23 km from Pacho to Zipaquirá, <i>B3538</i> (COL)
	11		COLOMBIA, CUNDINAMARCA: Km 34 of old Bogotá-Fusagasugá road, <i>B3543</i> (MO)
	11		COLOMBIA, CUNDINAMARCA: Km 36 of old Bogotá-Fusagasugá road, <i>B3543-B</i> (no voucher)
<i>F. hirtella</i> × <i>venusta</i>	11		COLOMBIA, CUNDINAMARCA: Km 39 of old Bogotá-Fusagasugá road, <i>B3547</i> (MO)
<i>F. lehmannii</i> Munz	11		ECUADOR, ZAMORA-CHINCHIPE: 27 km E of Loja, <i>B3200</i> (MO)
	11		ECUADOR, ZAMORA-CHINCHIPE: below El Retorno, <i>Mathias & Taylor 5200</i> (RSA) ²
<i>F. loxensis</i> Humboldt, Bonpland, & Kunth	11		ECUADOR, AZUAY: above Sayausí, <i>B3185</i> (MO)
	11		ECUADOR, LOJA: 5 km S of Saraguro, <i>B3192</i> (MO)
	11		ECUADOR, PICHINCHA: Panamerican Hway S of Quito, <i>B3233</i> (MO)
<i>F. macrophylla</i> I. M. Johnston	11	44	PERU, AYACUCHO: 58 km E of Tambo, <i>B3053</i> (MO)
<i>F. magdalenae</i> Munz			(Wright, 1978a) Cultivated plants from COLOMBIA, SE slopes Sierra Nevada de Santa Marta, Trombachuca Valley, <i>Wright</i> (RDG) ³
<i>F. mathewsii</i> J. F. Macbr.	11		PERU, CAJAMARCA: 39 km W of Celendín to Cajamarca, <i>B3602</i> (MO)
	11		PERU, AMAZONAS: 42 km E of Balsas to Leimebamba, <i>B3603</i> (MO)
	11		PERU, AMAZONAS: 51 km E of Balsas to Leimebamba, <i>B3606</i> (MO)
	11		PERU, AMAZONAS: 24 km above Leimebamba to Balsas, <i>B3612</i> (MO)
<i>F. nigricans</i> Linden	11		VENEZUELA, TRUJILLO: Agua Negra, 8 km SW of El Batatal, <i>B3093</i> (MO)
	11		VENEZUELA, TRUJILLO: 9 km SW of El Batatal, <i>B3095</i> (MO)

TABLE 4. Continued.

Taxon	<i>n</i>	<i>2n</i>	Collection Data or Reference
		c.22	VENEZUELA, TRUJILLO: 12 km from San Rafael to Trujillo, <i>B3104</i> (MO)
		22	VENEZUELA, MÉRIDA: above La Mucuy, <i>Berry in 1980</i> (MO)
<i>F. nigricans</i> × <i>venusta</i>	11		VENEZUELA, MÉRIDA: La Carbonera, <i>B3451</i> (MO)
	11		VENEZUELA, MÉRIDA: between La Azulita and La Carbonera, <i>B3453</i> (MO)
<i>F. orientalis</i> P. Berry	11		ECUADOR, ZAMORA-CHINCHIPE: 24 km E of Loja, <i>B3199</i> (MO)
	11		ECUADOR, NAPO: 10 km from Baeza to Cosanga, <i>B3246</i> (MO)
<i>F. pallescens</i> Diels	11		COLOMBIA, CAUCA: Km 41 W of Uribe, <i>B3570</i> (MO)
<i>F. petiolaris</i> Humboldt, Bonpland & Kunth	11		COLOMBIA, NORTE DE SANTANDER: 7 km above Pamplona to Bucaramanga, <i>B3533</i> (MO)
	11		COLOMBIA, CUNDINAMARCA: Cerro El Tablazo, <i>B3539</i> (MO)
	11		COLOMBIA, CUNDINAMARCA: E slopes Páramo de Choachí, <i>B3542</i> (MO)
	11		COLOMBIA, TOLIMA: 47 km W of Fresno, <i>B3558</i> (MO)
	11		COLOMBIA, TOLIMA: 48 km W of Fresno, <i>B3559</i> (MO)
<i>F. pilosa</i> Fielding & Gardner	11		PERU, AMAZONAS: 9 km E of Molinopampa to Mendoza, <i>B3618</i> (MO)
<i>F. polyantha</i> Killip	11		ECUADOR, CARCHI: 55 km W of Tulcán to Maldonado, <i>B3154</i> (MO)
<i>F. pringsheimii</i> Urban	22		DOMINICAN REPUBLIC, LA VEGA: Valle Nuevo, <i>B3707</i> (MO)
	c.22		DOMINICAN REPUBLIC, LA VEGA: Valle Nuevo, <i>B3709</i> (MO)
<i>F. rivularis</i> J. F. Macbr.	11		PERU, AMAZONAS: 9 km E of Molinopampa to Mendoza, <i>B3617</i> (MO)
<i>F. sanctae-rosae</i> Kuntze	11		BOLIVIA, LA PAZ: Chulumani, <i>Albert de Escobar 1303</i> (TEX)
	11		PERU (Huynh, 1965)
<i>F. sessilifolia</i> Benth.	c.11		ECUADOR, CARCHI: El Carmelo, <i>B3163</i> (MO)
	11		COLOMBIA, HUILA: Km 25 from Pitalito to Mocoa, <i>B3592</i> (MO)
<i>F. sylvatica</i> Benth.	11		ECUADOR, IMBABURA: 25 km W of Laguna Cuicocha, <i>B3171</i> (MO)
	11		ECUADOR, PICHINCHA: 25 km W of Chillogallo to Chiriboga, <i>B3237</i> (MO)
<i>F. tincta</i> I. M. Johnston	11		PERU, CUZCO: Km 131 of Cuzco-Paucartambo-Pilcopata road, <i>B2597</i> (MO)
	11		Source unknown, cultivated at Berkeley, California, 49.823 (UC) ²
<i>F. triphylla</i> L.	22	44	DOMINICAN REPUBLIC, LA VEGA: El Convento, 10 km S of Constanza, <i>B3701</i> (MO)
	22		DOMINICAN REPUBLIC, LA VEGA: ca. 1 km above El Convento, <i>B3702</i> (MO)
<i>F. vargasiana</i> Munz	11		PERU, CUZCO: Km 132 of Cuzco-Paucartambo-Pilcopata road, <i>B3000</i> (MO)
<i>F. venusta</i> Humboldt, Bonpland & Kunth	11		VENEZUELA, MÉRIDA: El Paramito, above La Carbonera, <i>B3450</i> (MO)
	11		COLOMBIA, CUNDINAMARCA: below Zipacón, <i>B3540</i> (MO)
	c.11		COLOMBIA, CUNDINAMARCA: Km 39 of old Bogotá-Fugasugá road, <i>B3548</i> (MO)

TABLE 4. Continued.

Taxon	<i>n</i>	<i>2n</i>	Collection Data or Reference
<i>F. verrucosa</i> Hartweg	22		VENEZUELA, TÁCHIRA: 6 km E of Zumbador to Queniquea, <i>B3417</i> (MO)
	c.20–22		COLOMBIA, CUNDINAMARCA: Km 34–35 to old Bogotá-Fusagasugá road, <i>B3535</i> (MO)
	22		VENEZUELA, TÁCHIRA: 5 km E of Las Porqueras to Pregonero, <i>B3662</i> (MO)
<i>F. vulcanica</i> André	22		ECUADOR, AZUAY: 13 km from Cuenca above Sayausí, <i>B3184</i> (MO)
		44	ECUADOR, AZUAY: 17 km from Cuenca above Sayausí, <i>B3187</i> (MO)
	22		ECUADOR, AZUAY: 18 km from Cuenca above Sayausí, <i>B3188</i> (MO)
		44	ECUADOR, AZUAY: 8 km S of Cumbe, <i>B3190</i> (MO)
	c.22		ECUADOR, NAPO: Papallacta, <i>B3245</i> (MO)
<i>F. wurdackii</i> Munz	11		PERU, AMAZONAS: vicinity of Leimebamba, <i>Hutchinson & Wright 4888</i> (UC) ²

¹ Numbers preceded by B were collected by the author.

² Counted by P. H. Raven from cultivated progeny.

³ A separate count of $2n = 44$ was obtained by Ching-I Peng from seeds sent to the Missouri Botanical Garden by J. O. Wright.

(see Table 4), comprising 43 species and five probable hybrids. Of these, 37 species yielded only diploid counts, five only tetraploid counts, and one species both diploid and tetraploid counts. *Fuchsia vulcanica* yielded four tetraploid counts and one possible diploid count. One of the putative hybrids, *Berry 3584* (MO), is tetraploid, forming 22 bivalents at metaphase I, and appears to be an allotetraploid derived from diploid populations of *F. corollata* and *F. caucana*. Four other hybrids were diploid and had normal meiotic pairing of 11 bivalents at metaphase I, although chromosomal bridges and fragments were observed in some cells at anaphase I. Since only limited field collected material was available for the hybrids, these results should be considered tentative and their interpretation doubtful.

Two of the six tetraploid or partly tetraploid species in sect. *Fuchsia* are disjunct and confined to the island of Hispaniola. One of these, *F. pringsheimii*, has nectaries and flowers uncharacteristic for sect. *Fuchsia*; its affinities are unclear, but it may share a common ancestor with *F. triphylla*, which is also endemic to Hispaniola but much more similar to other species of sect. *Fuchsia*. Of the South American species, *F. verrucosa* and *F. magdalenae* are also considered anomalous in sect. *Fuchsia*, because of their non-annular nectaries, as well as the extremely short floral tubes in *F. verrucosa*. The only species really typical of the main body of Andean species that are tetraploid are *F. vulcanica* and *F. corollata*. These are the only two of all the tetraploid species in the section that commonly have a large, though variable, proportion of triporate pollen grains. The other four species have entirely biporate grains, as do the other diploid species in the section. In the context of other polyploids that have been studied in the family Onagraceae (P. H. Raven, pers. comm.), this suggests that *F. vulcanica* and *F. corollata* might have become tetraploid recently, and that the other

four tetraploid species may be of more remote origin and have become stabilized. In *F. corollata*, both diploid and tetraploid populations are known, and the tetraploidy doubtless originated within the species. All species in sect. *Quelusia* and the single species of sect. *Kierschlegeria* are polyploid and have entirely triporate (or rarely four-porate) grains.

SYMPATRY AND INTERSPECIFIC HYBRIDIZATION

The evaluation of sympatry and interspecific hybridization in sect. *Fuchsia* is hampered by our still fragmentary knowledge of the population structure and distribution of many species. Despite many months of field studies and over 20,000 km of road travel in the Andes, I was not able to find living plants of 12 of the rarer species in the section. The broad latitudinal distribution of the section, the enormous stretches of cloud forest on the eastern slopes of the Andes that are virtually inaccessible, and the heavy rains that often cut off areas that do have roads are all factors that contribute to the difficulty of making field observations. The amount of known sympatry (discussed for each species in the systematic treatment) and of known or suspected interspecific hybridization (presented in Fig. 17) is therefore a conservative indication of the amount that likely occurs in nature.

Figure 17 shows that evidence for interspecific hybridization was found in 23, or just over a third, of the species in sect. *Fuchsia*, and species such as *F. nigricans* and *F. sanctae-rosae* were found to hybridize with three or four different species. Evidence for individual hybrid plants is discussed under the suspected parent species in the systematic treatment except for the example of *F. nigricans* in the following discussion. The main criterion used for recognizing naturally occurring hybrids was morphological intermediacy between the presumed parents, but decreased pollen stainability and local ecological factors such as habitat disturbance and the sympatric occurrence of the parental species were also considered to be correlated with hybrid origin in many cases. Pollen viability was estimated using the double staining malachite green/acid fuchsin/orange G stain of Alexander (1969), and stainability was found to be usually 90–100% in most species of *Fuchsia*. In interspecific hybrids it is usually considerably lower, but some suspected hybrids were almost fully fertile, while others were plants that had totally aborted pollen grains. Normal meiotic pairing was observed in several hybrids, and the sterility observed is not thought to be related to chromosomal reorganization. In most cases, however, morphological intermediacy and pollen stainability of less than 70% are considered strong evidence of hybrid origin. These criteria obviously limit the recognition of most hybrids to F_1 's, since backcross individuals are much harder to detect.

Although it is usually much easier to recognize living hybrid plants than dried ones, a number of hybrids were recognized from herbarium specimens, especially between morphologically well differentiated species. Because of low pollen stainability and the presence of unmistakable features of two distinct species, the type specimen of *Fuchsia caracasensis* (Fielding & Gardner, 1844) was recognized as a hybrid between *F. nigricans* and *F. gehrigeri*, both of which are known to grow near the type locality. *Fuchsia colombiana* (Munz, 1946) and *F. platypetala* (Johnston, 1939) were also probably based on hybrid individuals.

TABLE 5. Floral characters of *Fuchsia nigricans*, *F. venusta*, and a presumed hybrid.

	<i>F. nigricans</i> (Berry 3454)	Hybrid (Berry 3453)	<i>F. venusta</i> (Berry 3455)
Inflorescence	Subracemose to racemes 20 cm long	Subracemose to racemes 12 cm long	Subracemose
Pedicel length	3–5 mm	9–18 mm	25–28 mm
Ovary length	10–11 mm	9–13 mm	7–9 mm
Floral tube length	19–21 mm	30–37 mm	50–60 mm
Floral tube color	Lavender pink	Red pink	Orange red
Sepal length	8 mm	14–16 mm	16–18 mm
Petal length	8–10 mm	15–17 mm	18–20 mm
Petal color	Dark purple	Medium purple	Orange red
Fruit length	19–20 mm	14–15 mm	ca. 12 mm

genus (see Porcher, 1858; Hemsley, 1876; and Reiter, 1941). Although most of these hybrids were from other sections in the genus, *F. dominiana* (van Houtte, 1854) was an early hybrid between *F. macrostigma* and *F. denticulata*. Towards the end of the 19th century, the tetraploid *F. triphylla* was used in many inter-specific crosses (Wright, 1978b).

Numerous sympatric populations have been found with no evidence of hybridization, however. For example, a dense patch of *F. pringsheimii* was found growing along the edge of a potato field with scattered plants of *F. triphylla* at La Nuez, on the border of La Vega and Peravia Provinces, Dominican Republic, in December 1979. Despite the large sympatric populations and the fact that both of these species form hybrids on other parts of the island, no intermediates between these two distinctive species could be found. Only *F. triphylla* was flowering at the time, and it is possible that *F. pringsheimii* has a different flowering period at this locality. *Fuchsia tincta* and *F. vargasiana* are apparently closely related diploid species that occur side by side and flower together in southern Peru, yet no intermediate plants were detected. The same situation occurs with *F. macrophylla* and *F. macropetala* in central Peru. It is possible that hybrids between these species do occur but are not easily recognizable or were not flowering at the time the populations were examined. On the other hand, there may be prezygotic isolation mechanisms such as pollinator discrimination, especially in instances in which the sympatric species differ widely in flower size, but these are factors that have yet to be examined.

Despite the rarity of most hybrids, extensive hybrid populations were observed in two combinations. Suspected hybrids between *Fuchsia corollata* and *F. caucana* are numerous and widespread in southern Colombia. They occur in geographically intermediate areas between observed populations of the presumed parents, but at higher altitudes and in harsh subpáramo habitats. One of the probable hybrids was tetraploid. This indicates the possibility of well established hybrid populations that have occupied a new habitat and that might have originated as allotetraploids. A second case concerns probable hybrid swarms of *F. ampliata* and *F. vulcanica* in Prov. Cotopaxi, Ecuador. Very variable local populations have been found in heavily disturbed roadside areas, and these outnumber the presumed parental populations.

TABLE 6. Pollen stainability of putative hybrids of *Fuchsia nigricans* and representatives of sympatric parental populations.

Collection	Stainability
<i>F. nigricans</i> (Berry 3454)	81.8% (500 grains)
Hybrid (Berry 3453)	34.0% (500 grains)
<i>F. venusta</i> (Berry 3455)	81.0% (500 grains)
<i>F. nigricans</i> (Bernardi 653)	81.6% (1000 grains)
Hybrid (Bernardi 652)	28.5% (1000 grains)
<i>F. cf. venusta</i> (Bernardi 664)	69.0% (1000 grains)
Other hybrids <i>F. nigricans</i> × <i>F. venusta</i>	
Ricardi & Hernandez 5722	4.0% (500 grains)
Bernardi s.n.	less than 10% ¹
<i>F. gehrigeri</i> (Berry 3128)	88.3% (600 grains)
Hybrids × <i>F. nigricans</i> :	
Berry 3129	5.3% (300 grains)
Aristeguieta & Medina 3670	8.6% (500 grains)
Linden 368 (OXF)	21.3% (400 grains)
<i>F. nigricans</i> (Fosberg & Core 21550)	84.0% (500 grains)
Hybrid (Fosberg 21556)	28.6% (500 grains)
Hybrid (Fosberg 21558)	0.2% (1000 grains)
<i>F. sessilifolia</i> (Fosberg 21560)	94.7% (1000 grains)
<i>F. nigricans</i> × <i>F. putumayensis</i> :	
Robinson 138	0.6% (500 grains)

¹ Estimated due to poor stain differentiation.

The relative rarity of most hybrids found indicates that unless large or numerous populations are carefully examined, many hybrids will be overlooked, and thus that the likelihood of finding hybrid individuals is strongly dependent on the sampling intensity. The Venezuelan Andes was the only area that was intensively studied. Four species are sympatric there, *F. gehrigeri*, *F. nigricans*, *F. venusta*, and *F. verrucosa*, and all possible hybrid combinations were found except those involving *F. verrucosa*. Since this is the only tetraploid species in the group and is distantly related to the others, it is probable that postzygotic barriers to hybridization exist between *F. verrucosa* and its sympatric congeners.

Fuchsia nigricans possesses several distinctive characters such as purple petals, canescent pubescence, and elongate, tapered ovaries. Because of these features, hybrids involving this species are relatively easy to detect. These features, together with characters such as the sympatric occurrence of the parent species, field observations in some cases, and reduced pollen stainability (Table 6), were used to compile the following list and discussion of putative hybrids with this species.

Putative hybrids involving *Fuchsia nigricans*

Fuchsia nigricans × *F. venusta*. Berry 3453 (MO, VEN): Venezuela, Edo. Mérida, Dpto. Campo Elias, 4 km below San Eusebio on the road to La Azulita, wet roadbanks, 4 April 1979. The morphologically intermediate characters of this

TABLE 7. Comparison of morphological characters in *Fuchsia nigricans*, *F. gehrigeri*, and presumed hybrids.

	<i>F. gehrigeri</i> (Berry 3128)	Hybrid (Berry 3129)	Hybrid (Aristeguieta & Medina 3670)	<i>F. nigricans</i> (Average Values)
Stem pubescence	Subglabrous to strigillose	Densely canescent to strigillose	Canescent	Densely canescent
number of secondary veins	5–7	10–12	13	12–16
Leaves/node	3–4	2–3	3	3
Pedicel length	25–35 mm	9–12 mm	8–15 mm	3–10 mm
Floral tube length	51–54 mm	30–33 mm	30–35 mm	14–22 mm
Petal length	14–15 mm	10–12 mm	13–14 mm	5–10 mm
Petal color	Red	Purple	Dark red	Dark purple
Stigma exsertion above anthers	9–10 mm	2 mm	9 mm	0–2 mm
Fruit shape	Subglobose	Cylindrical	—	Cylindrical
Seed size (L × W)	2–2.5 × 1.2 mm	1.5–2 × 1 mm (mostly aborted)	—	1.5 × 0.8 mm

collection are shown in Table 5 and in Figure 33, and the reduction in pollen stainability is evident in Table 6. Both parental species occurred side by side at this locality in wet roadside thickets (Fig. 4), though *F. nigricans* was locally more abundant. The hybrid showed strong vegetative growth and was also intermediate in pubescence and leaf texture. Meiotic preparations from *Berry 3453* had normal formation of 11 bivalents, as did samples from the parental species nearby.

Bernardi 652 (NY): Venezuela, Edo. Mérida, Monte Zerpa, cloud forest, 2,300 m, 21 June 1953. Both parental species were collected in the vicinity by the same collector on the same date, and *Bernardi 652* has flowers like *F. nigricans* except for a longer (35 mm) floral tube and mostly elliptic leaves like *F. venusta*.

Other specimens with hybrid characters similar to those described above and with low pollen fertility include *Bernardi s.n.* (NY; Venezuela, without locality, 15 Feb. 1957), *Bernardi 6119* (MER; Venezuela, Edo. Mérida, Selva La Vagabunda), and *Ricardi & Hernández 5772* (MER; Venezuela, Edo. Mérida, Valle Grande, 2,300–2,500 m).

Fuchsia nigricans × *F. gehrigeri*. *Aristeguieta & Medina 3670* (NY, VEN): Venezuela, Edo. Trujillo, Dpto. Boconó, Visún, south of Las Mesitas, ca. 2,400 m, Aug. 1958. *Berry 3129* (MO, VEN) was collected at the same site in Sept. 1978. These collections probably come from the same population, which formed a dense thicket about 5 m² in a sunny hollow with extensive vegetative reproduction occurring by stem shoots. Just 10 m away, several plants of *F. gehrigeri* were growing in shade along the forest edge. No plants of *F. nigricans* were seen in the vicinity, but they undoubtedly occur in the area.

The presumed hybrids are clearly morphologically intermediate between the indicated species (Table 7), and their pollen stainability is in both cases less than 10% (Table 6). Buds of *Berry 3129* were examined cytologically and had 11 bivalents at metaphase I, with occasional bridges and fragments at anaphase I. Though ripe fruits were produced in *Berry 3129*, most of the seeds were aborted.

TABLE 8. Comparison of morphological characters in *Fuchsia nigricans*, *F. sessilifolia*, and presumed hybrids.

	<i>F. nigricans</i> (Fosberg & Core 21550)	Hybrid (Fosberg 21556)	Hybrid (Fosberg 21588)	<i>F. sessilifolia</i> (Fosberg 21560)
Leaves/node	2–3	3–4	3–4	4
Leaf shape	Broadly elliptic- obovate	Oblanceolate-ob- ovate	Elliptic	Narrowly elliptic- lanceolate
Blade length (max.)	9.5 cm	15 cm	13 cm	18 cm
Petiole length	15–20 mm	8–10 mm	6–15 mm	5–11 mm
Leaf margin	Subentire to den- tulate	Serrulate	Denticulate	Serrate to serrulate
number of secondary veins	10–11	17–18	13–16	15–19
Floral tube color	Dull crimson	Green red to crimson	Crimson	Green
Petal color	Dark purple	Crimson to pur- ple	Purple	Red
Inflorescence	Spreading, race- mose	Drooping, pani- culate	Drooping, sub- paniculate	Drooping, panicu- late

Two other probable hybrids with *F. gehrigeri* are *Benítez de Rojas* 1887 (VEN; Venezuela, Edo. Trujillo, road from Boconó to Trujillo) and *Linden* 368 at OXF (OXF; Venezuela, Edo. Mérida, between Mendoza and Timotes, 1843). This latter collection was used as the type specimen of *F. caracasensis* Fielding & Gardner (Sert. Pl. t. 29. 1844) but has highly inviable pollen (Table 6) and a series of intermediate characters between *F. nigricans* and *F. gehrigeri* such as long floral tubes, elongate ovaries, unequal leaf bases, and oblong leaves. The same collection number at P was used to describe *F. nigricans*, but this and the duplicates at BM, G, K, LE, TCD, US, and W are clearly different, with high pollen stainability and no indication of intergradation with *F. gehrigeri*.

Fuchsia nigricans × *F. sessilifolia*. *Fosberg* 21556 (RSA, US): Colombia, Chocó, 7 km N of Carmen de Atrato, bank above trail, 2,675 m, 6 March 1944, “calyx varying from greenish red to crimson, corolla from crimson to purple.” Also *Fosberg* 21558 (RSA, US): 8 km N of Carmen de Atrato, steep bank above trail, same date, “calyx crimson, corolla purple, with 21560 (= *F. sessilifolia*) but colors not intergrading.” Both of these collections have highly reduced pollen stainability and characters clearly intermediate between *F. nigricans* and *F. sessilifolia* (Tables 6 and 8). The variability and intermediate flower color noted above is also indicative of their hybrid origin. *Fuchsia nigricans* was collected along the same trail at 2,500 m, and *F. sessilifolia* grew together with *Fosberg* 21588. Although the flower size and shape of the two parental species are very similar, the very different leaves and flower color offer excellent indicators for analyzing presumed hybrids. The combination of such distinctive characters as the subsessile, lanceolate leaves of *F. sessilifolia* and the purple petals of *F. nigricans* leave little doubt as to the parentage of the presumed hybrids.

The largely triporate pollen grains found in *Fosberg & Core 21550* (*F. nigricans*) are noteworthy. The four diploid counts of *F. nigricans* from Venezuela were made from plants with biporate grains. Triporate grains in *Fuchsia* are sometimes indicators of polyploidy, so there may be tetraploid populations of this taxon in Colombia. If so, this would perhaps explain the extremely low pollen stainability of the presumed hybrids between these rather closely related species.

Fuchsia nigricans $\times$ *F. putumayensis*. *Robinson 138* (COL, K, US): Colombia, Dept. Valle, Río Bravo, northwest of Darién, 4,200 ft., 28 July 1962. This plant has almost entirely inviable pollen (Table 6). The purple petals and elongate ovaries indicate genetic input from *F. nigricans*. The subnitid, sulcate-nerved upper leaf surface is typical of *F. putumayensis*, however, as are the divergent, slender petals. The rachis is too long for that species, though, and the leaves are often ternate as in *F. nigricans*. Both presumed parent species have been collected in the general area, and the low altitude indicated on Robinson's label is consistent with the parentage of *F. putumayensis*, which grows at lower altitudes (from ca. 1,200–1,800 m) than any other species in the Cordillera Occidental of Colombia.

All of the preceding evidence supports a high degree of interfertility in most species of sect. *Fuchsia* and indicates that natural interspecific hybridization is a common, but not ubiquitous, phenomenon between sympatric species. When hybrids do occur, they are usually rare and localized, but two examples were given that illustrate the evolutionary potential of populations of hybrid origin that have become better adapted to certain habitats than the parent species. The increased genetic recombination afforded by interspecific hybridization has probably been of considerable adaptive significance in sect. *Fuchsia* during the late Tertiary uplift of the Andes and especially in the Pleistocene, when new and disturbed habitats were formed as a result of severe climatic fluctuations.

THE EVOLUTION OF *FUCHSIA* SECT. *FUCHSIA*

One of the main questions addressed by this study is how and why so many more species evolved in *Fuchsia* sect. *Fuchsia* than in other sections of the genus. Through the evidence presented in the preceding sections, it is possible to attempt answers to this question.

We can begin by distinguishing the importance of extrinsic or physical factors from ones related to the plants themselves. Prior to the Neogene, the tropical Andes were probably too low for fuchsias to occur there. In the context of angiosperm evolution, the Andes are newly uplifted mountains, and they are furthermore composed of a number of distinct structural units. Starting in the Miocene, and especially during the Pliocene, they were strongly uplifted from the surrounding lowland tropical areas to give rise to a wide variety of new habitats over a very broad geographical area. Cool, montane forest habitats ("cloud forest" or "Andean forest") first appeared and increased in extension, followed by open, high elevation habitats ("puna" and "páramo"). In this way, large expanses of new, cool habitats in the tropics became available for adaptation by lowland, tropical taxa, or for colonization by previously cool-adapted organisms

from temperate areas. The latter possibility was shown to be the case in *Fuchsia*, which had a probable Paleogene origin in temperate South America.

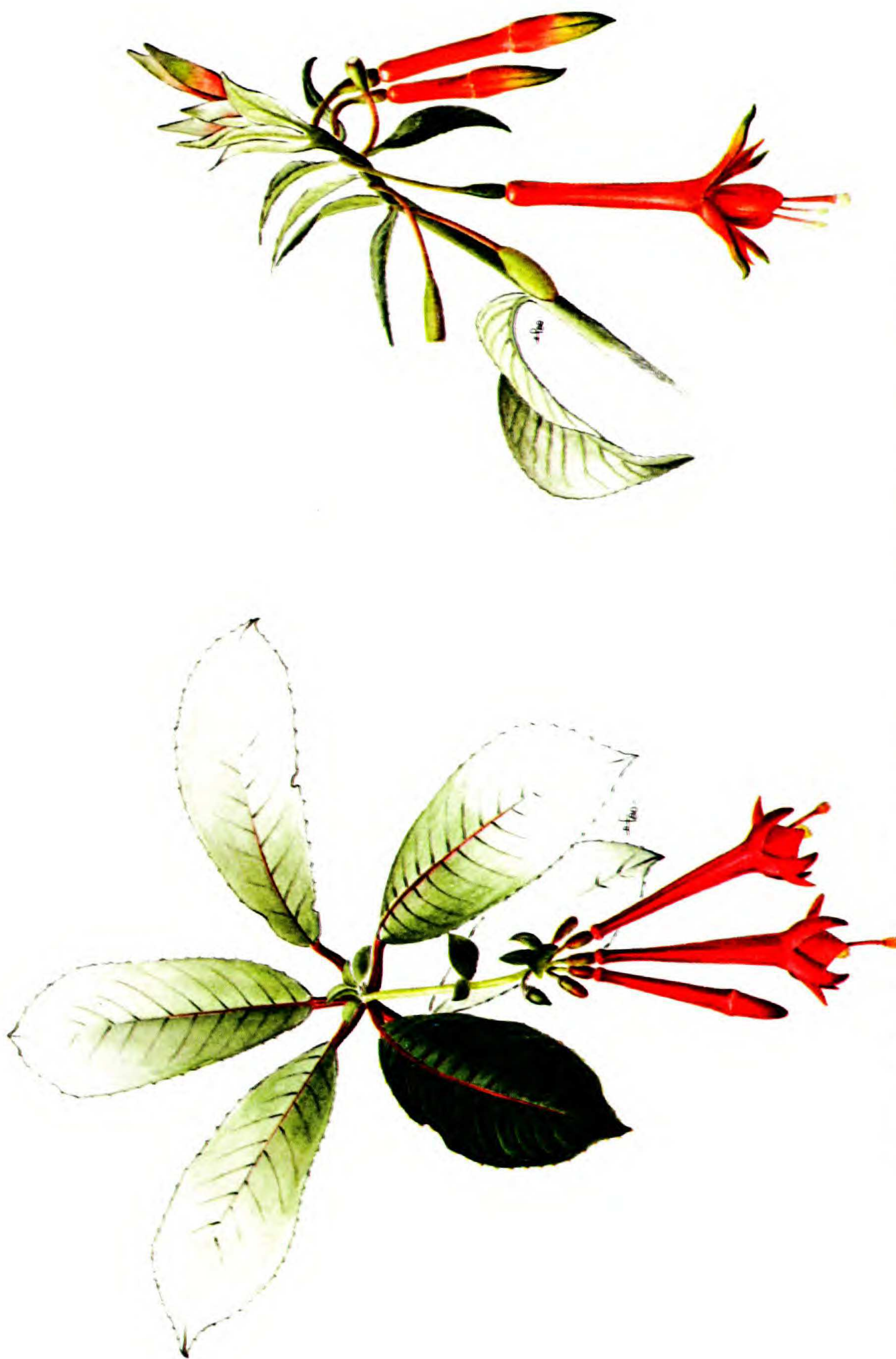
The other key extrinsic factor in understanding plant evolution in the Andes is the series of strong climatic changes that occurred as a result of Pleistocene glaciations, whose magnitude in the tropics went largely unrecognized until the last two decades. As discussed in Raven (1980), drastic climatic shifts (such as those caused by the uplift of the Andes and by Pleistocene glaciations) produce new or fundamentally altered environments, thereby setting the stage for rapid speciation. This can also be described as an increase in the ecological opportunity for the establishment of new immigrants or new adaptive gene combinations (Mayr, 1963).

The ways to exploit and adapt to these changes in the physical conditions of the Andes are seen in the different reproductive strategies that the organisms inhabiting them have evolved. *Fuchsia* is a good colonizer as a result of its self-compatibility and dispersal by birds. This is probably how the genus migrated into the tropical Andes and reached isolated islands such as Tahiti and Hispaniola. Especially when new Andean forest habitats were developing, major jumps within the tropical Andes may have occurred by long-distance dispersal. Populations established in this way may have formed the nuclei of the different species groups that we recognize today, and which are usually centered in a specific geographic area. Bird dispersal is an important factor in local migrations as well, such as those discussed previously between the different structural units of the Andes.

Certain ecological adaptations were favorable to the diversification of sect. *Fuchsia* in the Andes. Of the two sections of the genus now present in the tropical Andes, sect. *Hemsleyella* became adapted to seasonal conditions and developed a basically epiphytic or lithophytic habit, whereas sect. *Fuchsia* is more generalized and remains more or less aseasonal in mesic, terrestrial habitats. Section *Fuchsia* has over four times as many species as sect. *Hemsleyella* over roughly the same geographical range.

Because members of sect. *Fuchsia* are restricted to mesic habitats where more or less constant moisture is available, they have not radiated strongly into different ecological zones. Nonetheless, many species have become adapted to different altitudinal tolerances and can remain spatially isolated on the same mountain range. Montane cloud forests are dynamic communities where natural disturbances such as landslides, tree falls, clearings, and water courses abound. These are the main areas where sect. *Fuchsia* occurs, though man-made disturbances have recently added a new dimension to this system. The particularly flexible breeding system of sect. *Fuchsia* is well adapted to such disturbed habitats; plants are loosely growing, mostly scandent shrubs that are modally outcrossing but self-compatible and have a relatively high and constant flowering rate, yet they are capable of considerable vegetative reproduction. These are adaptations that would have been particularly advantageous during the Pleistocene, when habitat disturbances were increased by the glacial cycles.

Adaptation to hummingbird pollination has been another important factor in the evolution of sect. *Fuchsia*. Hummingbirds can maintain their flower-visiting activity throughout the year in cool, wet habitats whereas insects are far more



FIGURES 18–19. Illustrations of *Fuchsia* sect. *Fuchsia*.—18 (Left). *Fuchsia crassispula* P. Berry, from Berry 3553 (MO), Tolima, Colombia. Scale: floral tubes of open flowers are 46 mm long.—19 (Right). *Fuchsia denticulata* Ruiz & Pavón, from Berry & Aronson 3048 (MO), Cuzco, Peru. Scale: floral tube of the open flower is 43 mm long.



FIGURES 20–22. Illustrations of *Fuchsia* sect. *Fuchsia*.—20 (Upper half). *Fuchsia abrupta* I. M. Johnston, from Berry & Aronson 3077 (MO), Junín, Peru. Scale: floral tubes of largest open flowers are 45 mm long.—21 (Lower left). *Fuchsia nigricans* Linden, from Berry 3095 (MO), Trujillo, Venezuela. Scale: floral tubes of open flowers are 20 mm long.—22 (Lower right). *Fuchsia scabriuscula* Benth., from Berry & Escobar 3178 (MO), Pichincha, Ecuador. Scale: floral tubes of open flowers are 23 mm long.

limited in their activity. Like *Fuchsia*, hummingbirds have diversified mainly in the tropical Andes. Although the dynamics of hummingbird pollination in *Fuchsia* have not been examined, it is likely that at least in some species the differences in floral tube length restrict interspecific pollination by hummingbirds.

Enough cytological data is now available to state that sect. *Fuchsia* is chromosomally homogeneous, and species tend to be largely interfertile. Six species are tetraploid or partly so, but these occur mostly in outlying geographical areas or have morphological features anomalous in the section. The presence of numerous naturally occurring hybrids, the near normal meiotic behavior of those hybrids examined, and the existence of at least two cases of widespread populations of probable hybrid origin, indicate that interspecific hybridization on the homoploid level, rather than polyploidy, has probably played an important role in the evolution of the section.

It is now recognized that the lack of internal barriers to hybridization in plants, especially in perennials, is more the rule than the exception, and that the main differences between plant groups occur in the nature and strength of external mechanisms that restrict interspecific hybridization (Raven, 1980). In other groups in the Onagraceae that have radiated very recently, such as *Epilobium* in New Zealand (Raven & Raven, 1976) and *Oenothera* in South America (Dietrich, 1978), interspecific hybridization has been the key feature in the differentiation of new taxa, but the different units now recognized as species have remained distinct mostly through predominant autogamy, strong radiation into widely different habitats, and the unique genetic system of complex structural heterozygotes in the case of *Oenothera*. *Fuchsia* sect. *Fuchsia*, on the other hand, has not been able to radiate much beyond the cloud forest zone, and it is primarily outcrossing, with specialized hummingbird pollination, rather than autogamous. Other cloud forest groups such as *Monochaetum* (Almeda, 1978) have reproductive systems similar to *Fuchsia*, and these are likely to prove quite common in other groups of woody Andean angiosperms.

INTERSPECIFIC RELATIONSHIPS IN *FUCHSIA* SECT. *FUCHSIA*

The lack of any major morphological, cytological, or ecological differentiation in all but a few of the 61 species in sect. *Fuchsia* precludes a formal division of the species into series or other subsectional taxonomic categories. The mode of evolution in sect. *Fuchsia* appears to have been strongly reticulate, permitting only clusters of rather closely related species to be recognized. In general, it has not been possible to discriminate between more primitive or advanced species, and this may in part be due to the recent differentiation of the section.

Munz (1943) informally divided sect. *Fuchsia* into two lines, species with long floral tubes and those with short floral tubes. Groups were circumscribed based on inflorescence structure. The shape of petals and floral tubes was used to further subdivide the species. Because a continuous range of floral tube lengths from 3 to 130 mm exists in the species of sect. *Fuchsia*, it is arbitrary to divide them into two groups on this basis. Pairs of closely related species are known, such as *F. polyantha* and *F. sessilifolia*, in which one species is short-tubed and the other long-tubed.



FIGURES 23–26. Illustrations of *Fuchsia* sect. *Fuchsia*.—23 (Upper left). *Fuchsia ampliata* Benth., from Berry & Escobar 3234 (MO), Pichincha, Ecuador. Scale: floral tube of open flower is 45 mm long.—24 (Upper right). *Fuchsia venusta* Humboldt, Bonpland & Kunth, from Berry 3292 (MO), Táchira, Venezuela. Scale: floral tubes of open flowers are 48 mm long.—25 (Lower left). *Fuchsia harlingii* Munz, from Berry & Escobar 3206 (MO), Loja, Ecuador. Scale: floral tubes of open flowers are 48 mm long.—26 (Lower right). *Fuchsia caucana* P. Berry, from Berry 3590 (MO), Huila, Colombia. Scale: floral tube of open flower is 40 mm long.



FIGURES 27–30. Illustrations of *Fuchsia* sect. *Fuchsia*.—27 (Upper left). *Fuchsia ferreyrae* P. Berry, from Berry & Aronson 3073 (MO), Junín, Peru. Scale: floral tubes of open flowers are 26 mm long.—28 (Upper right). *Fuchsia verrucosa* Hartweg, from Berry 3286 (MO), Táchira, Venezuela. Scale: ovary is 11 mm long.—29 (Lower left). *Fuchsia triphylla* L., from Berry, Smith & Mejía 3701 (MO), La Vega, Dominican Republic. Scale: floral tube of open, lowermost flower is 36 mm long.—30 (Lower right). *Fuchsia pringsheimii* Urban, Berry, Smith & Mejía 3711 (MO), La Vega, Dominican Republic. Scale: floral tubes are 27 mm long.



FIGURES 31–33. Illustration and photographs of *Fuchsia* sect. *Fuchsia*.—31 (Left). *Fuchsia ceracea* P. Berry, from *Berry & Aronson 3081* (MO), Huánuco, Peru. Scale: sepals of the left hand flower are 29 mm long. Note the tender, concave bracts sheathing the base of the flowers.—32 (Upper right). The hummingbird *Chlorostilbon swainsonii* visiting *Fuchsia triphylla*. Both species are endemic to Hispaniola. Photograph by Donald Dod, taken between Constanza and Valle Nuevo, Prov. La Vega, Dominican Republic.—33 (Lower right). Flowers of two sympatric species of sect. *Fuchsia* and their hybrid. Upper flower is from *F. venusta* (Berry 3455, MO), the lower flower is from *F. nigricans* (Berry 3454, MO), and the middle flower (Berry 3453, MO) is from a natural hybrid between the above species. Note the intermediate size and color of the hybrid flowers. The three plants were found growing together in roadside thickets between La Carbonera and La Azulita, at 2,200 m, Edo. Mérida, Venezuela, in June 1979; their habitat is illustrated in Figure 4, and further evidence of the probable hybrid origin of *Berry 3453* is given in the text.

Whereas my key to the species of sect. *Fuchsia* closely follows Munz's scheme, a different approach has been used here to recognize species groups. Floral position, tube length, and petal shape are used here, but these characters were analyzed in more detail and were supplemented by ecological, geographical, cytological, and vegetative characters. Instead of a dichotomous, linear system, 14 different species groups that are intended to reflect the evolutionary relationships between the species more realistically are proposed. These species groups are first approximations and should not be regarded as formal taxonomic categories.

The order of the species groups is not necessarily meant to reflect any particular evolutionary sequence, though the short-tubed, axillary-flowered species may be more primitive and are placed at the beginning. Those species of doubtful affinity are included with the closest probable species group, and those of unknown affinities are placed together in a final group. Each species group is followed by a brief summary of its principal characteristics.

1) *Fuchsia decussata* species group: *F. decussata*, *F. ferreyrae*, *F. fontinalis*, and *F. sanctae-rosae* (Fig. 55). Short-tubed, mostly axillary flowers with narrow petals. The first three are closely related and have divaricate or predominantly horizontal branching and denticulate leaves, but *F. fontinalis* has flowers tending towards a paniculate inflorescence. *Fuchsia sanctae-rosae* has thicker, less constricted floral tubes, nearly entire leaves, more erect branching and is more distantly related to the first three species. Peru and Bolivia.

2) *Fuchsia loxensis* species group: *F. loxensis*, *F. scabriuscula*, *F. steyermarkii* (Fig. 56). A very loosely connected group with exclusively axillary flowers, short to medium floral tubes, and rather broad petals. *Fuchsia loxensis* is treated as a polymorphic species whose taxonomy is not fully understood; its round petals and large leaves suggest that it may be close to the *F. petiolaris* species group. *Fuchsia scabriuscula* has no clear relative and has very few flowers and opposite, reticulate leaves, unlike the other members of this group. The linear leaves of *F. steyermarkii* are unique in the section, but its flowers resemble those of *F. loxensis* more than any other species. Colombia and Ecuador.

3) *Fuchsia nigricans* species group: *F. nigricans*, *F. sylvatica*, *F. pallescens*, *F. orientalis*, and *F. glaberrima* (Fig. 57). Characterized by mostly short-tubed, axillary to racemose flowers with narrow petals, short pedicels, and cylindrical ovaries and fruits. The first three species are closely allied and each has petals that are considerably darker than the sepals. The transitional stages of axillary to racemose inflorescences are particularly evident in these species. The last two species are closely related and have definite racemes with persistent bracts and prominent stipules, but the flowers and leaves of *F. orientalis* link the two subgroups together. Venezuela to northern Peru.

4) *Fuchsia macrophylla* species group: *F. macrophylla*, *F. macropetala*, *F. ovalis*, and *F. pilosa* (Fig. 56). The first two species are closely related and, with *F. ovalis*, have lateral or axillary inflorescences rather than the usual terminal or subterminal ones (Fig. 40). Though *F. pilosa* has a terminal inflorescence, it is

placed here because of the close similarity of leaves, flowers, and pubescence to *F. ovalis*. Short-tubed, except for *F. macropetala*. Peru.

5) *Fuchsia putumayensis* species group: *F. putumayensis*, *F. lehmannii*, *F. andrei*, *F. cuatrecasasii*, and *F. abrupta* (Fig. 58). Short to long floral tubes with reddish orange flowers, and delicate, usually recurved petals. Flowers mostly densely packed in short, terminal racemes with lanceolate, recurved, or deciduous bracts. Pedicels usually divergent. *Fuchsia abrupta* is long-tubed and has elongate inflorescences; its affinities are unclear, but it is placed here because of its strongly divergent pedicels, delicate, recurved petals, and mostly opposite leaves, which are found in most of the above species. Colombia to central Peru.

6) *Fuchsia petiolaris* species group: *F. petiolaris*, *F. corollata*, *F. caucana*, *F. ayavacensis*, *F. vulcanica*, and *F. ampliata* (Fig. 59). Long-tubed, axillary flowers with various shaped, often pubescent petals. High altitude, often subpáramo habitats. A well delimited group, but individual species are similar and poorly defined. Populations of *F. vulcanica* and *F. corollata* are tetraploid. Additional cytological and population sampling is needed, especially for *F. vulcanica*, *F. corollata*, and *F. petiolaris*. Southernmost Venezuela to northern Peru.

7) *Fuchsia venusta* species group: *F. venusta*, *F. rivularis*, *F. gehrigeri*, *F. llewelynii*, *F. scherffiana*, and *F. confertifolia* (Fig. 60). Medium- to long-tubed flowers with narrow petals, in the upper axils or in incipient racemes with mostly long pedicels. The first two species are closely related and have a common climbing habit, crispate petals, subcoriaceous elliptic leaves, and slightly hairy petals. They are probably linked to the *F. petiolaris* species group through *F. gehrigeri*. Since the last three species are known only from a few fragmentary collections, their affinities are unclear. *Fuchsia confertifolia* has very distinctive reduced leaves, but they are subcoriaceous as in the first two species, and the more or less crispate petals and axillary to racemose inflorescence place it closest to this group. *Fuchsia llewelynii* and *F. scherffiana* are probably closely allied and are placed here on the basis of their subcoriaceous leaves, long pedicels, and medium-long flowers. Venezuela to northern Peru.

8) *Fuchsia denticulata* species group: *F. denticulata*, *F. austromontana*, *F. harlingii*, *F. cochabambana*, *F. macrostigma*, and *F. magdalenae* (Fig. 61). Long-tubed, axillary flowers with thick, firm, mostly cylindric floral tubes. Pedicels stout; petals variable, but often drying purplish; anthers large (3–6 mm long). A distinctive group in its solitary, stout flowers. The first three species are closely related. *Fuchsia cochabambana* has funnelform flowers grouped at the tips of branches, but they are more or less thick-tubed and have purple-drying petals as in the first two species. *Fuchsia macrostigma* has thick, axillary flowers, but long, curved, narrowly funnelform floral tubes with large, spreading petals and a massive quadrangular stigma. Though *F. magdalenae* seems clearly to belong to this group because of its strong resemblance to *F. denticulata*, it has an entirely different type of nectary from the rest of the species in sect. *Fuchsia*. It is also tetraploid and isolated on the Sierra Nevada de Santa Marta range. Colombia to Bolivia.

9) *Fuchsia simplicicaulis* species group: *F. simplicicaulis*, *F. ceracea*, *F. coriaticifolia*, and *F. sanmartina* (Fig. 62). Very rare, viny shrubs with long to very long floral tubes and petals generally (much) shorter than the sepals. The first two species are unique in the genus with involucre of short-pedicellate flowers and thin membranous, concave, sessile bracts. The latter two species have racemose inflorescences but seem to be derived from, or at least closely related to the first two. The bracts of *F. coriaticifolia* are smaller than those of the first two species, but they are still sessile and slightly concave; the basal flowers of the inflorescence are verticillate; the upper flowers are alternate. The inflorescences of *F. sanmartina* have mostly alternate flowers, and the bracts are lanceolate, short-petiolate, and mostly deciduous. Central Peru.

10) *Fuchsia sessilifolia* species group: *F. sessilifolia* and *F. polyantha* (Fig. 63). Two closely related species, one with short, bicolored flowers and the second with long, uniformly red flowers. Leaves quaternate, lanceolate, subsessile, nitid dark green. Flowers in well-branched terminal panicles. Colombia and Ecuador. *Fuchsia sessilifolia* shares several important characters with the *F. nigricans* species group.

11) *Fuchsia tinctoria* species group: *F. tinctoria*, *F. furfuracea*, and *F. vargasiana* (Fig. 62). A closely related group with opposite, ovate leaves and pilose pubescence; short, few-flowered, terminal, corymbiform racemes with long pedicels. Endemic to southern Peru and Bolivia.

12) *Fuchsia boliviana* species group: *F. boliviana*, *F. corymbiflora*, *F. wurdackii*, and *F. mathewsii* (Figs. 63 and 65). A loosely united group with large, pubescent leaves and terminal, long racemes or few-branched panicles of long-tubed flowers. *Fuchsia boliviana* is distinctive in its arborescent habit, wide ecological tolerances, reflexed sepals, and early petal dehiscence. The leaves of these species are mostly opposite or ternate, which distinguishes them from the following group. Northern Peru to northern Argentina (excluding the naturalized range of *F. boliviana*).

13) *Fuchsia dependens* species group: *F. dependens*, *F. hirtella*, *F. hartwegii*, *F. crassistipula*, *F. canescens*, and *F. cinerea* (Fig. 66). Pubescent, mostly quaternate leaves, narrow petals, flowers mostly paniculate and long-tubed. The first three species are very closely related, differing mainly in tube and petiole length. *Fuchsia crassistipula* is also allied to these species but has unusually thick, persistent stipules and frequently more than four leaves per whorl. *Fuchsia canescens* has thick floral tubes and intermediate axillary to racemose flowers. Though the flowers of *F. cinerea* are all axillary, the leaves and individual flowers are very similar to *F. dependens*, and it cannot be placed in any other species group. Colombia and Ecuador.

14) Anomalous species: *F. triphylla*, *F. pringsheimii*, and *F. verrucosa* (Figs. 65 and 67). All three of these species are tetraploid and cannot be placed close to any of the preceding groups. Except for its disjunct distribution, low-growing habit, and suberect inflorescences, *F. triphylla* has no features in which it differs substantially from the Andean species. *Fuchsia pringsheimii*, like *F. triphylla*, is

endemic to the island of Hispaniola. It has very small leaves, broad, obconic floral tubes, and large, emarginate petals unlike any other species in sect. *Fuchsia*. It also possesses a non-annular, lobed nectary that is clearly atypical of the section. Although it does not closely resemble *F. triphylla*, the two do hybridize on Hispaniola, and they may have evolved from a distant, common ancestor.

Fuchsia verrucosa also has an atypical non-annular nectary (Figs. 46 and 47) as well as an extremely reduced floral tube. Although it occurs in Venezuela and Colombia, well within the main range of sect. *Fuchsia*, it shows no clear affinities to any of the species in that group, and, unlike all other members of sect. *Fuchsia*, it has smooth viscin threads (J. Nowicke, pers. comm.).

MORPHOLOGY AND ANATOMY

HABIT

All species in sect. *Fuchsia* are basically perennial shrubs or lianas. Although two species, *F. pallescens* and *F. triphylla*, can flower while still remaining essentially herbaceous, woody-stemmed plants are more common. *Fuchsia boliviana* is usually arborescent and can reach a height of 6 m with a stem diameter of up to 5 cm. A number of species such as *F. glaberrima*, *F. pilosa*, *F. tinctoria*, *F. vargasiana*, and *F. verrucosa*, are suberect and rarely exceed a height of 2–3 m. Many others, however, can surpass this height and then become scandent or climbing. Since plants of sect. *Fuchsia* usually grow in moist thickets, they can rely on neighboring trees or brush for support. The closely related *F. dependens* and *F. hartwegii* commonly occur as semierect hedgerow shrubs in disturbed or semicultivated sites, but in suitable areas such as streamside forests, they occur as lianas clambering well into the canopy of small trees. *Fuchsia denticulata* is a widely distributed species that grows as erect shrubs in the drier parts of its range but as scandent or climbing plants in cloud forest. A few species, such as *F. venusta* and *F. rivularis*, are especially prone to climbing and often have long, flexible stems trailing along the ground until suitable support such as a tree or tangle is found (Fig. 3). They reach heights of 10–15 m by means of long, flexuous-pendant branches. One species, *F. ceracea*, is known only as a liana with long, drooping branches. A few herbarium sheets of species such as *F. petiolaris* and *F. nigricans* record their habit as epiphytic, but all plants of sect. *Fuchsia* that I examined in the field were rooted in the ground.

STEMS

Carlquist's (1975) comparative analysis of Onagraceae wood anatomy showed that species of *Fuchsia* have relatively long and wide vessel elements, as expected of mesomorphic species. Unlike most Onagraceae, however, *Fuchsia* lacks interxylary phloem. This character state is undoubtedly primitive in the family and is shared only by *Ludwigia* and *Hauya*, two other relatively unspecialized genera (Carlquist, 1975). Within the genus, sect. *Fuchsia* lacks the tuberous-thickened stems frequently found in the related sects. *Ellobium* and *Hemsleyella*.

The most useful external stem characters in sect. *Fuchsia* are the branching pattern, cross-sectional configuration, color, and bark texture on older stems.

Branching pattern. Most species are loosely branched near the base or distal to a relatively short main stem. The branches are usually ascending when young but then become spreading or drooping when they elongate and age. *Fuchsia fontinalis* and *F. ferreyrae* commonly have horizontally spreading secondary branches. The related *F. decussata* is unique in the section with its well developed branching system and short, strongly divaricate tertiary branchlets. The higher order branches of *F. confertifolia* are very much shortened and ascending. *Fuchsia scabriuscula* is often low-growing with divergent to nearly prostrate branches. Those species with a climbing habit often have a flexuous main stem and long, poorly branched secondary branches that vary from divergent to drooping or pendant. A few species such as *F. glaberrima*, *F. pilosa*, and *F. sessilifolia* generally have few or no secondary branches.

Stem cross-section. The majority of species in sect. *Fuchsia* have terete branchlets, but some have branchlets that are noticeably ridged, which can be a diagnostic field character. The upper stems of *F. crassistipula* have a series of ridges and deep furrows that correspond in number to the petioles of the whorl of leaves above it, but the ridges begin to disappear towards the basal part of the internode. Another species with conspicuously ridged stems is *F. canescens*, and a few species such as *F. venusta* lack the prominent ridges of the above species, but have trigonous or angled stems.

Stem color and bark texture. Light green or reddish stems are typical of most species of *Fuchsia*. Dull bluish purple stems are characteristic of *F. venusta*, as are smooth purple stems for *F. harlingii* and *F. rivularis*. Rusty colored stems occur at times in *F. mathewsii*, *F. decussata*, and *F. fontinalis*, as a result of their ferrugineous-pilose pubescence. Young stems of *F. verrucosa* are somewhat tuberculate, and *F. llewelynii* has numerous spinescent projections on the stems and pedicels.

Older, woody stems have three basic bark types. The most common is the sort of flaky, exfoliating bark typical of *F. decussata* and thick-stemmed species such as *F. hartwegii*, *F. gehrigeri*, *F. loxensis*, and *F. boliviana*. Also widespread is the finely fissured, grayish tan bark characteristic of *F. andrei*, *F. hirtella*, and *F. putumayensis*. Finally, a third smooth bark that splits off in a few long, wide strips occurs in *F. harlingii*, *F. rivularis*, and *F. magdalenae*.

PUBESCENCE

The few glabrous or nearly glabrous species in sect. *Fuchsia* are *F. ceracea*, *F. polyantha*, *F. putumayensis*, and *F. cuatrecasasii*. In the remaining species, the pubescence can be quite variable between populations, but it is usually constant enough to distinguish species with fundamentally different pubescence types. Trichomes in *Fuchsia* are all simple and one- to few-celled (R. Keating, pers. comm.). The basic pubescence types used in the species descriptions include *puberulent* (minute, erect hairs), *canescent* or *incanous* (dense, fine grayish white hairs), *hirsute* (erect, moderately stiff hairs ca. 1 mm long), *hispid* (stiff, erect hairs more than 1 mm long), *pilose* (soft, suberect hairs less than 1 mm long), *strigose* ($\pm$ appressed hairs 0.5–1 mm long), *strigillose* ($\pm$ appressed hairs less than 0.5 mm long), and *villous* (loose, soft hairs ca. 1 mm long). Additional color

or texture terms (e.g., ferrugineous, pruinose) are used to supplement the basic types described above.

LEAVES

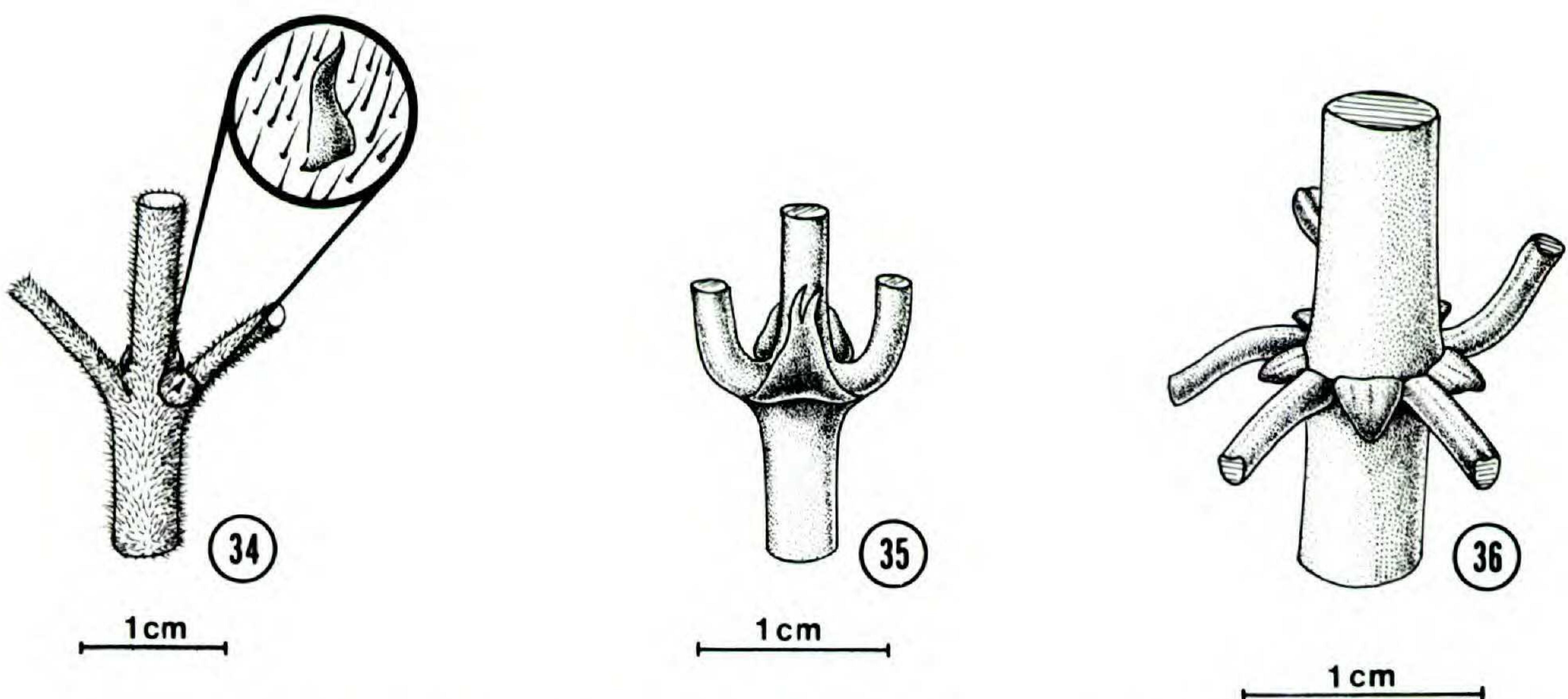
The leaves of sect. *Fuchsia* are simple, opposite or whorled, usually petiolate, stipulate, and pinnately veined. The secondary veins depart from the midvein at a right to acute angle and generally curve apically toward the margin, either joining the superadjacent secondary to form marginal loops and an intramarginal vein (brochidodromous type of Hickey, 1973) or diminishing toward the margin without forming marginal loops with the superadjacent secondary (essentially the eucamptodromous type of Hickey, 1973). The secondary veins are commonly more or less sulcate on the dorsal surface and prominent on the ventral side. The number of secondary veins is often a diagnostic leaf character, but comparison between species should be based on similar basal leaves. A diagnostic character of *F. verrucosa* is the clearly impressed brochidodromous venation. *Fuchsia steyermarkii* and *F. coriacifolia* are unusual in their almost inconspicuous secondary veins. The secondary veins of *F. caucana* have an unusually acute angle of divergence, and they remain straight until nearly the margin of the leaf. *Fuchsia scabriuscula* and some populations of *F. sylvatica* have conspicuous higher order venation that gives a rugulose-reticulate appearance to the leaf surface.

Leaf anatomy studies by R. Keating (1980, in prep.) have determined the following basic leaf structure in *Fuchsia*: one trace, unilacunar nodes; protruding midribs with a semicircular primary vasculature; blade with a thick, single-celled cuticle, single palisade and mesophyll layers; stomata present only on the ventral surface, and raphides in vertical bundles in the palisade layer. In dried specimens the raphide bundles appear to be parallel to the leaf surface.

Stipules. The stipules in sect. *Fuchsia* lose much of their diagnostic value once the plants are dried. The commonest stipule type is thin, narrowly lanceolate, not connate, and early deciduous (Fig. 34). Some species, however, have connate stipules or a mixture of separate and connate ones, making them interpetiolar and reminiscent of those of the Rubiaceae (Fig. 35). By far the most distinctive stipule type in the genus is found in *F. crassistipula*: the stipules on the lower leaf nodes are large, persistent, incrassate, connate, recurved, and with a thickened midvein (Fig. 36). Other species with thick, prominent, and persistent stipules are *F. canescens*, *F. glaberrima*, *F. orientalis*, *F. ovalis*, and *F. pilosa*. *Fuchsia abrupta* usually has large, connate stipules, but they are not thickened as in the above species. *Fuchsia wurdackii* has unusually long (3–5 mm), pale, chartaceous, blunt-tipped stipules.

Leaf margin. The margins of *Fuchsia* leaves typically have glandular, “fuchsoid” teeth (Hickey, 1980). These teeth may be inconspicuous, however, so that the margin appears entire in species such as *F. putumayensis*, *F. macrophylla*, and *F. cuatrecasasii*. Other species in the section are remotely to markedly denticulate or serrulate. Strongly serrulate leaves characterize *F. cochabambana* and *F. sessilifolia*, and the margins of *F. confertifolia* and *F. steyermarkii* are recurved.

General leaf characters. Mature leaves in sect. *Fuchsia* vary in length from



FIGURES 34–36. Main stipule types in *Fuchsia* sect. *Fuchsia*.—34. The most common type of separate, lanceolate stipules, *F. boliviana*, from living material growing at El Portachuelo, D.F., Venezuela.—35. Connate, interpetiolar stipules, *F. verrucosa*, Berry 3662 (MO).—36. Incrassate, connate stipules of *F. crassistipula*, Berry 3553 (MO).

1 to 27 cm. *Fuchsia confertifolia* has tiny, coriaceous leaves less than 15 mm long, and the leaves of *F. decussata* and *F. pringsheimii* rarely exceed 4 cm long. Species with leaves exceeding 10 cm long include *F. macrostigma*, *F. macrophylla*, *F. glaberrima*, *F. boliviana*, and *F. sessilifolia*. Leaves of most species range from 3 to 10 cm long and 1.5 to 4 cm wide and are membranous. *Fuchsia steyermarkii* is a very distinctive species with linear leaves just 3 mm wide. A few species are readily distinguishable by their nearly sessile leaves (*F. cochabambana*, *F. confertifolia*, *F. sessilifolia*, and *F. polyantha*). Ovate leaves are unusual in the section and characterize the *F. tincta* species group as well as many plants of *F. boliviana*. Unusual leaf textures are found in *F. coriacifolia* (firm-coriaceous), *F. ceracea* (waxy-pruinose), and *F. pallescens* (thin membranous). A few species are commonly found that have leaves strongly purple-flushed on the under surface. The best examples of this unusual coloration are *F. triphylla*, *F. tincta*, and *F. glaberrima*.

The number of leaves per node varies in many species, but it is quite constant in certain groups. Exclusively opposite leaves are found in *F. corymbiflora*, *F. cuatrecasasii*, *F. putumayensis*, *F. tincta*, and *F. verrucosa*. Predominantly quaternate leaves occur in the *F. dependens* and *F. sessilifolia* species groups.

INFLORESCENCES

Floral position and arrangement is one of the best diagnostic characters in sect. *Fuchsia*, and definite trends can be recognized in certain groups. The four basic types of floral arrangement in sect. *Fuchsia* are 1) axillary, 2) verticillate or involucrate, 3) racemose, and 4) paniculate (Figs. 37–41). Intermediate arrangements occur between all these types, especially between axillary and racemose flowers. The position of the inflorescence is also important; most are terminally disposed, but the *F. macrophylla* species group has distinctly axillary racemes or panicles.

Axillary flowers are considered the least advanced type, since they are the basic type found in the rest of the genus and family. Four sections of *Fuchsia* have flowers that are exclusively axillary (*Quelusia*, *Encliandra*, *Skinnera*, and *Kierschlegeria*), and only two small, probably advanced sections are exclusively racemose or paniculate (*Jimenezia* and *Schufia*). Section *Hemsleyella* is a specialized section that has axillary and racemose flowers, these last derived from axillary flowers through the shortening of the terminal internodes (Berry, unpublished). In the three species of sect. *Ellobium*, the most generalized species has axillary flowers, the intermediate one has racemose flowers, and the most advanced species has lateral panicles (Breedlove et al., 1982).

The strictly involucrate type of inflorescence (Fig. 38) is rare in sect. *Fuchsia*, found only in two species of the *F. simplicicaulis* species group. These species are unique in having sessile, concave bracts. The apparently derived *F. coriaticifolia* maintains the similar sessile (but only slightly concave) bracts; its inflorescence has elongated into a raceme with the basal flowers verticillate and the distal ones alternate. In *F. simplicicaulis*, a verticillately branched system of terminally arranged involucre sometimes occurs.

Plants with axillary flowers that intergrade into terminal racemes are relatively common, especially in the *F. nigricans* species group. Rachis length is a diagnostic character in species that have inflorescences. The *F. putumayensis* species group is characterized by very short, corymbiform racemes with narrow bracts and often divergent pedicels. Species such as *F. boliviana*, *F. wurdackii*, and *F. pilosa* have elongate racemes.

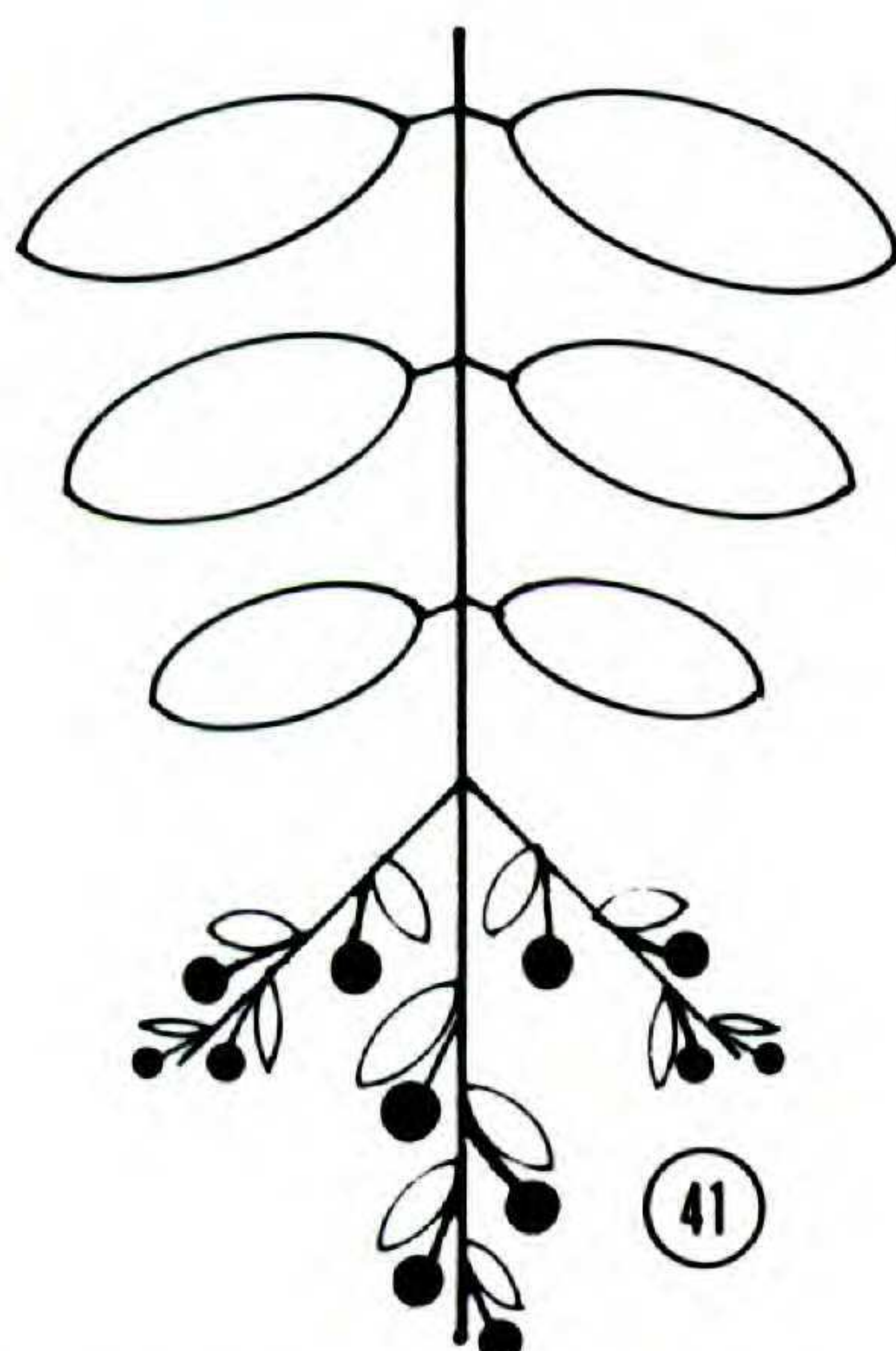
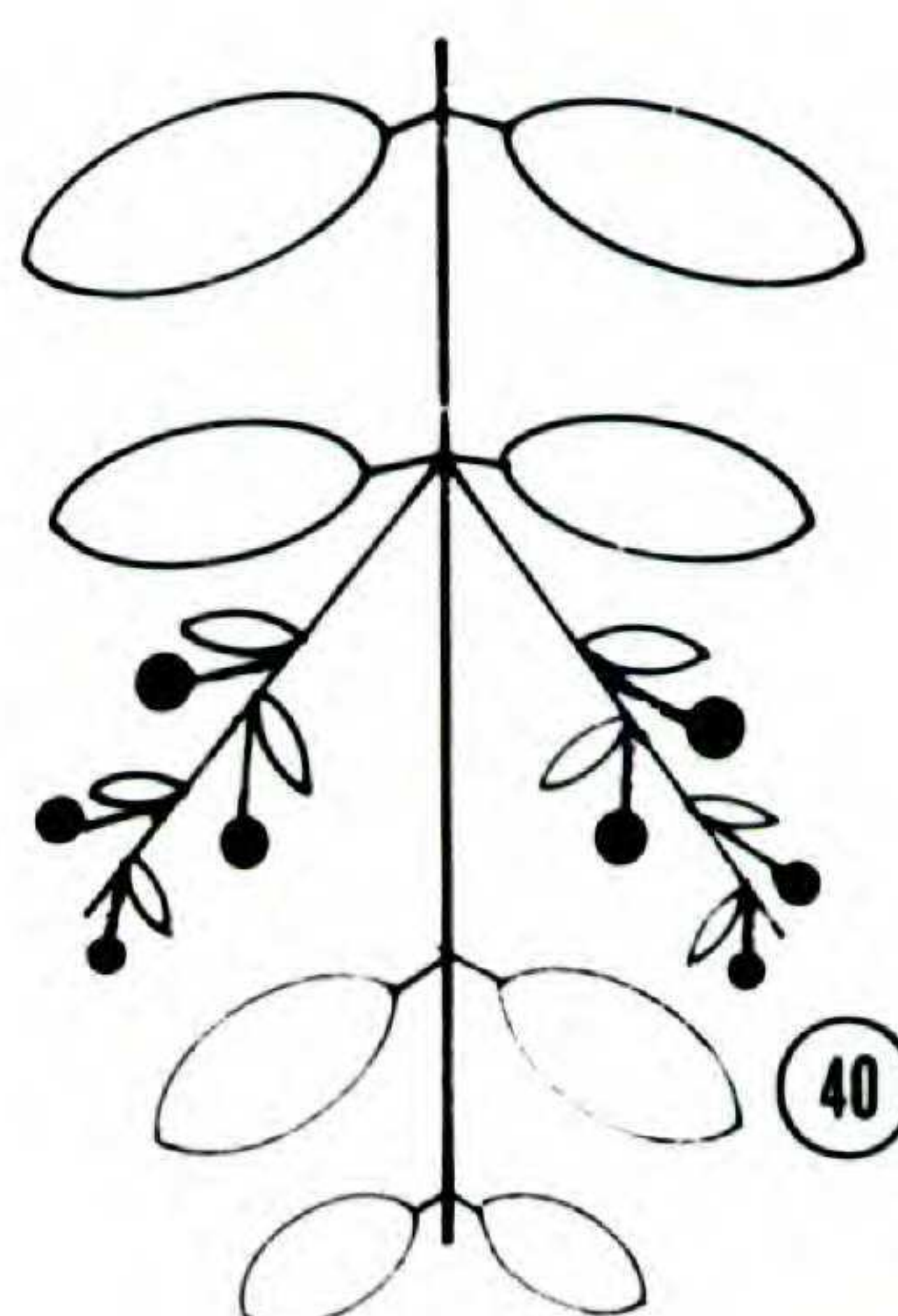
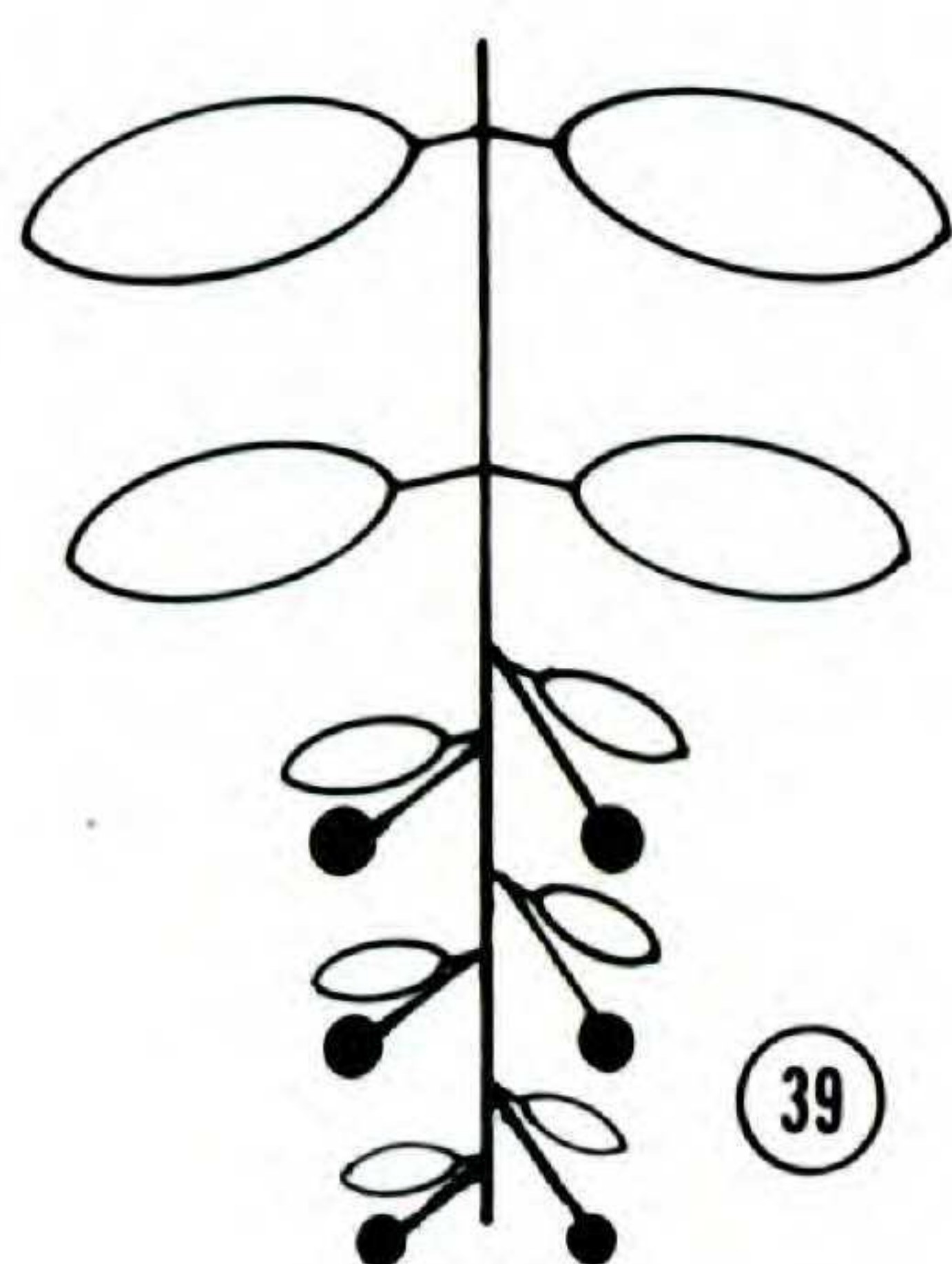
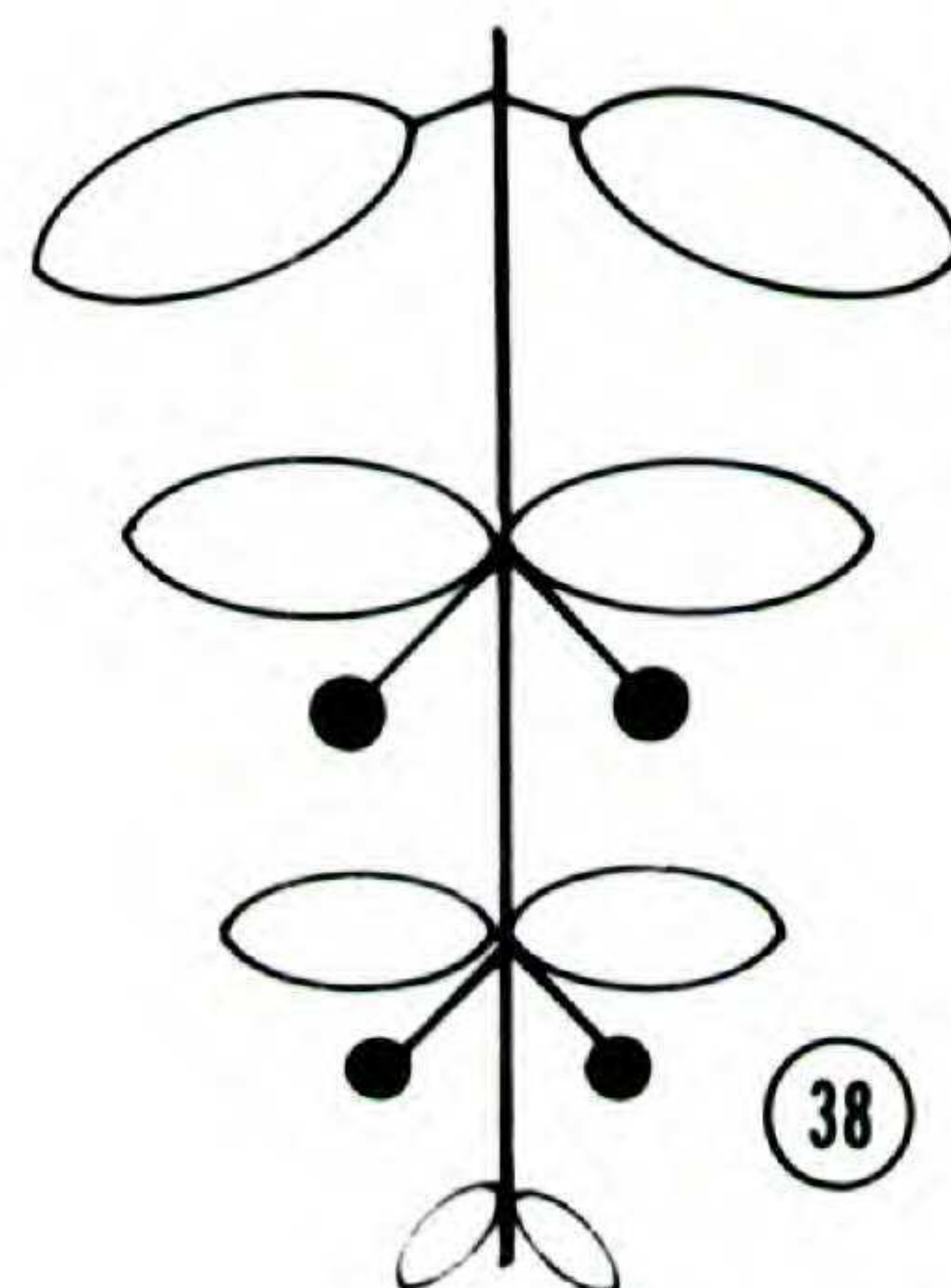
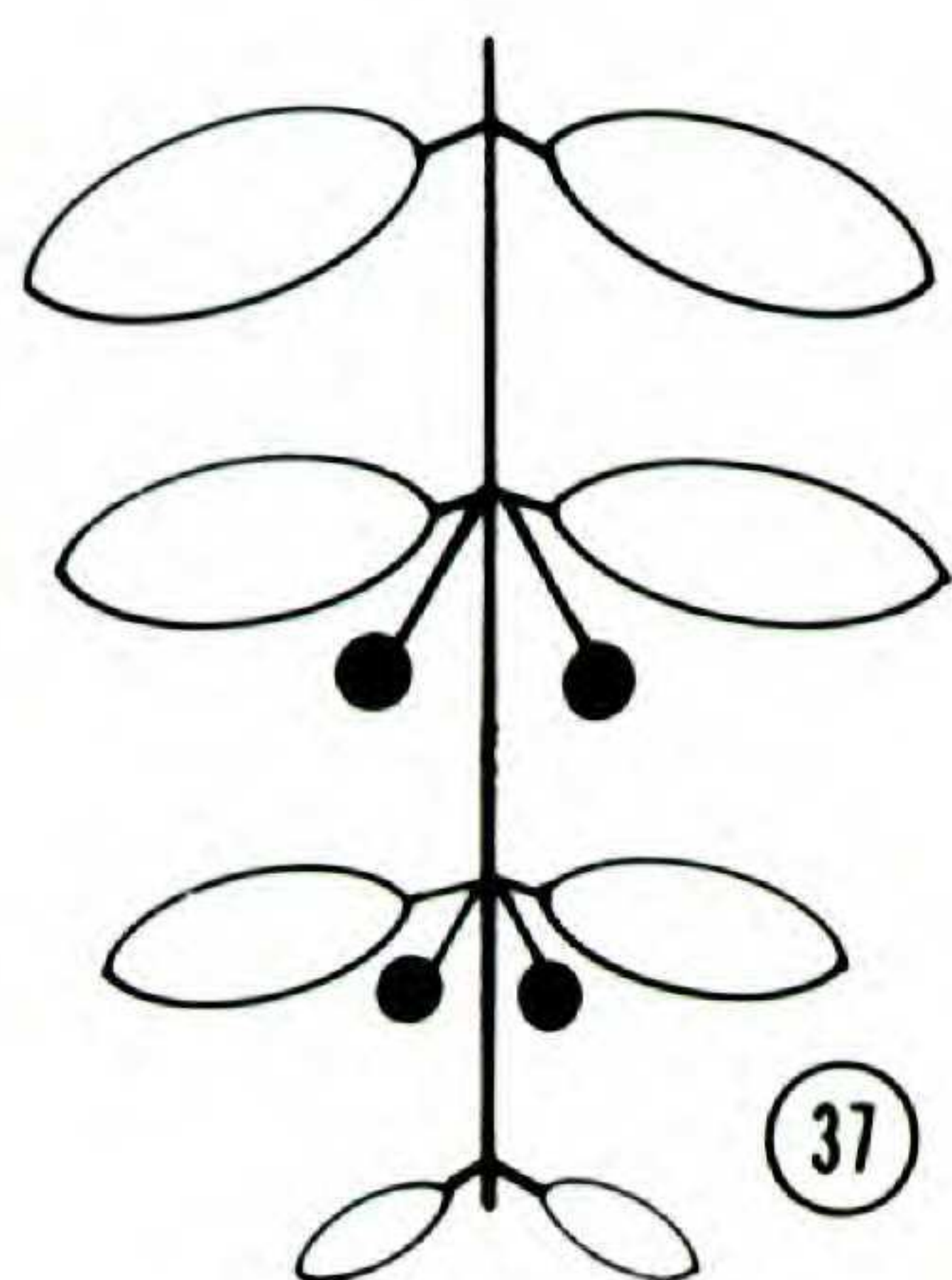
The inflorescences of the *F. dependens* and *F. sessilifolia* species groups are almost entirely paniculate, and intermediate racemose to paniculate inflorescences are found scattered in several species groups, as in *F. ovalis*, *F. boliviana*, *F. mathewsii*, and *F. fontinalis*.

FLORAL CHARACTERS

Floral tube and sepals. In all species of *Fuchsia* there is an elongate floral tube above the inferior ovary. The tube length is measured from the top of the ovary to the rim of the tube on which the sepals, petals, and stamens are inserted. The length of the floral tube in the section varies from 3 mm (*F. verrucosa*) to 130 mm (*F. ceracea*), but the length is constant within fairly narrow limits for most species and is a valuable taxonomic character.

Flowers in sect. *Fuchsia* are divergent to drooping, but never erect. Most species have floral tubes that are somewhat nodose or bulbous at the base around the nectary, creating a nectar reservoir inside the tube. This character varies with tube shape and there is little or no bulging at the base in more or less cylindric tubes such as are commonly found in the *F. denticulata* species group. On the other hand, strongly nodose floral tubes occur in *F. triphylla* and *F. ferreyrae*, both species with marked constrictions in their lower portions.

An important field character is the texture and thickness of the floral tube. Most species have tubes that are membranous and well under 1 mm thick when fresh. The *F. denticulata* species group and a few other species such as *F. canescens* and *F. coriaticifolia* have firm-fleshy floral tubes with thick, spongy walls 1–2 mm thick when fresh. Thick tubes may well have evolved in connection with



FIGURES 37–41. Basic inflorescence types in *Fuchsia* sect. *Fuchsia*.—37. Axillary flowers; present in several species groups.—38. Involucrate flowers with sessile bracts; found only in the *F. simplicicaulis* species group.—39. Terminal racemes; found in several species groups.—40. Lateral racemes; found only in the *F. macrophylla* species group.—41. Terminal panicles; typical of the *F. dependens* species group.

protection against flower piercers. Tetragonous floral tubes are typical of *F. verrucosa*, and less markedly angled tubes are found in *F. pringsheimii* and part of the *F. putumayensis* species group.

The sepals are valvate in bud and generally resemble the floral tube in texture and thickness. Presence and length of sepal tips in buds varies. *Fuchsia pilosa*, *F. rivularis*, and *F. macrostigma* have free, spreading sepal tips in bud. At anthesis, the angle of the sepals is suberect to divergent in most species, but both *F. ampliata* and *F. boliviana* are immediately recognizable because their sepals become fully reflexed soon after anthesis.

Petals. Important petal characters are shape, size relative to the sepals, presence of pubescence, texture, surface, and angle at anthesis. Only a few species have pubescent petals, and in these cases the hairs are distributed on the outer side. *Fuchsia petiolaris* has the most consistently hairy petals, which vary from having a few villous hairs along the midnerve to having scattered or dense, puberulent hairs. Hairs can also be found on petals of some populations of *F. gehrigeri*, *F. harlingii*, *F. venusta*, and *F. rivularis*.

The petal surface of *F. boliviana*, *F. venusta*, and *F. rivularis* is usually ridged, and the petal margin can be somewhat undulate or crispate. The petal margins of *F. magdalenae* are often irregular in the distal half, with a small mucronate tip. *Fuchsia boliviana* is the only species that has petals that regularly dehisce before the tube drops off. Unusual petal shapes include the trullate (trowel-shaped) petals in *F. canescens*, rhomboid petals in *F. corollata*, and large, obovate, emarginate petals in *F. pringsheimii*.

Flower color. Flower color is an important field character, and species that are often difficult to distinguish with dried herbarium specimens are immediately separable in the field by their distinctive coloration patterns. Though all species have some basic red coloration, many species are characterized by orange, lavender, purple, or scarlet colors. Others have color gradations within the flower. *Fuchsia nigricans*, for example, has pinkish sepals and floral tubes but contrasting dark purple petals and filaments (Fig. 21). Several species, like *F. denticulata*, have green sepal tips (Fig. 19). This species usually has more or less orange petals that contrast with the waxy red or pink floral tube. *Fuchsia ferreyrae* has deep blue violet flowers, a color unique in the section (Fig. 27). Other distinctively colored flowers are those of *F. caucana* (purple lavender, with darker petals), *F. sessilifolia* (pale greenish floral tubes with red petals), and *F. pallescens* (pale pink floral tubes with red purple petals). In the *F. denticulata* species group, the petals characteristically dry with purple streaks that are not evident when the flowers are fresh.

Androecium. The eight stamens are all erect and biseriate, and the antesepalous filaments are always longer than the antepetalous ones. In the species descriptions, the measurements of the antesepalous filaments are always listed first, followed by the antepetalous ones.

Gynoecium. The inferior ovary is four-locular with unspecialized axile placentation (Eyde & Morgan, 1973). The numerous ovules are anatropous and biseriate in each locule. Ovaries are either terete or quadrangular in transection. Style

pubescence can vary in certain species, so it is only of relative value. Stigmas are smooth-surfaced with a wet stigmatic surface (Raven, 1979a), and they vary in shape from clavate to capitate or obconic. The stigma always separates into four lobes, but these may be very slight as in *Fuchsia denticulata*, or they may consist of 4 large, prominent mounds as in *F. macrostigma*.

Nectaries. Nectaries recently have been found to be a highly diagnostic character at the sectional level (Breedlove et al., 1982). Section *Fuchsia* is characterized by having an annular nectary that is not found in any other section. This nectary is formed by a ringlike disc that surrounds the style at the base of the tube. The ring is mostly free from the tube or attached only at its base and can usually be dissected out of the flower intact; it is entire in some species or four-, eight-, or irregularly lobed in others (Figs. 42 and 43). All other sections have nectaries that are mostly or completely fused to the floral tube. Three species in sect. *Fuchsia* have anomalous nectary types, however. *Fuchsia pringsheimii* has an irregularly lobed nectary that is fully adnate to the floral tube (Fig. 44); its flowers are anomalous in sect. *Fuchsia* in other respects, and it is isolated on the island of Hispaniola. *Fuchsia magdalenae* seems to belong to the *F. denticulata* species group based on general floral characters, but its nectary consists of a smooth or slightly ridged band adnate to the tube, similar to the nectaries in sects. *Hemsleyella* and *Ellobium* (Figs. 45 and 48). *Fuchsia verrucosa* is yet another anomalous species in sect. *Fuchsia*, and its nectary is composed of four separate, antesepalous lobes adnate to the floral tube (Figs. 46 and 47). All three of these species are tetraploid, have biporate pollen, and are distinctive from other members of the section.

FRUITS

The berries of sect. *Fuchsia* vary in shape from cylindrical-fusiform to globose. When ripe, they usually have a reddish coloration clearly related to dispersal by birds. Seeds in sect. *Fuchsia* vary approximately twofold in size and are generally of little taxonomic value. Because they number from ca. 50 to 200 per fruit, the seeds are laterally compressed and irregularly oblong-triangular in shape, with considerable variation within the same fruit. Bright red seeds, rather than the typical tan brown ones, are sometimes found in fruits of *F. caucana*, *F. scabriuscula*, and *F. sessilifolia*.

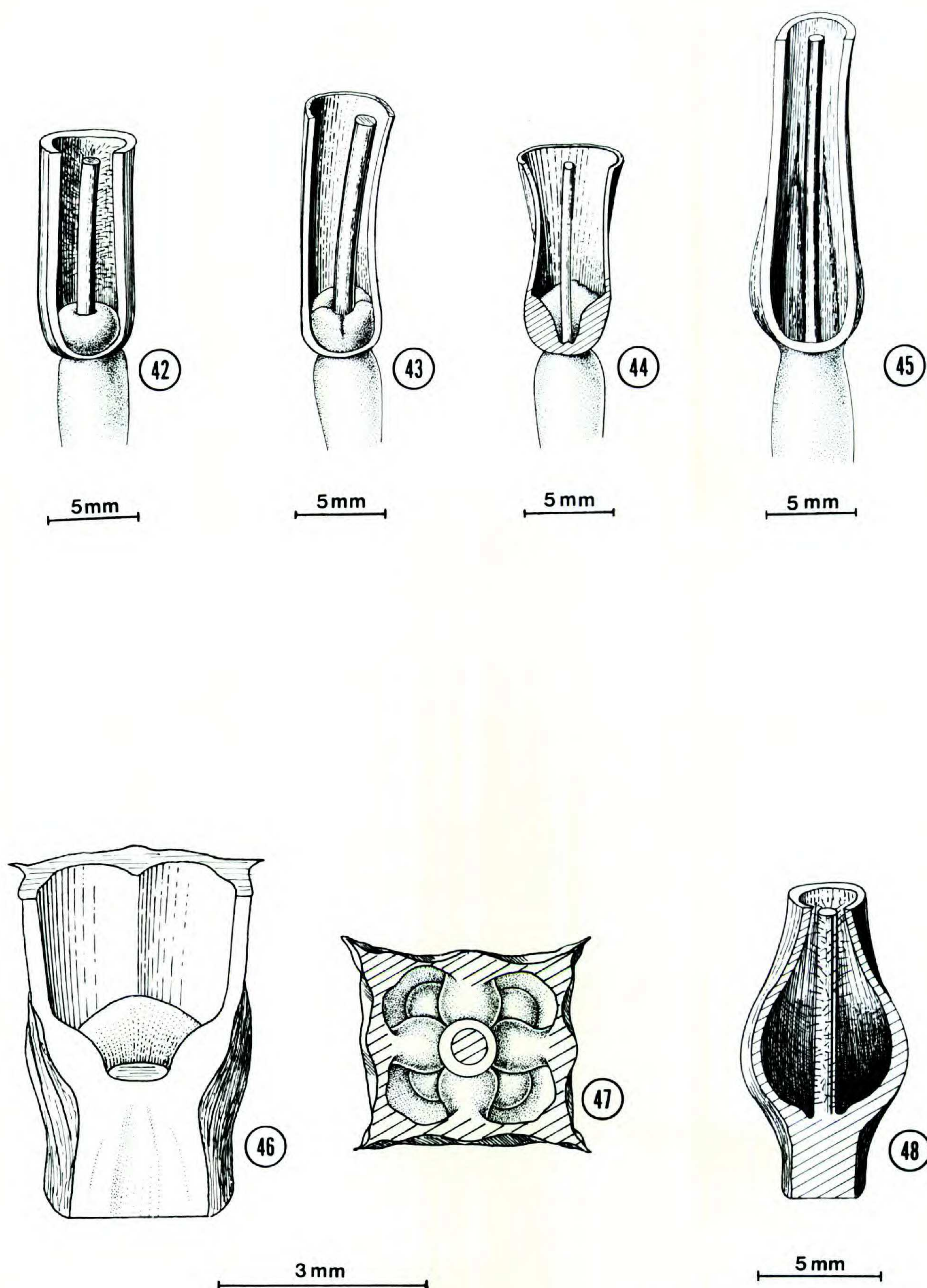
POLLEN

Onagraceae pollen is probably the most distinctive of the angiosperms, because of the viscin (exine) threads, protruding apertures, and atypical (for the dicots) structure of the exine.

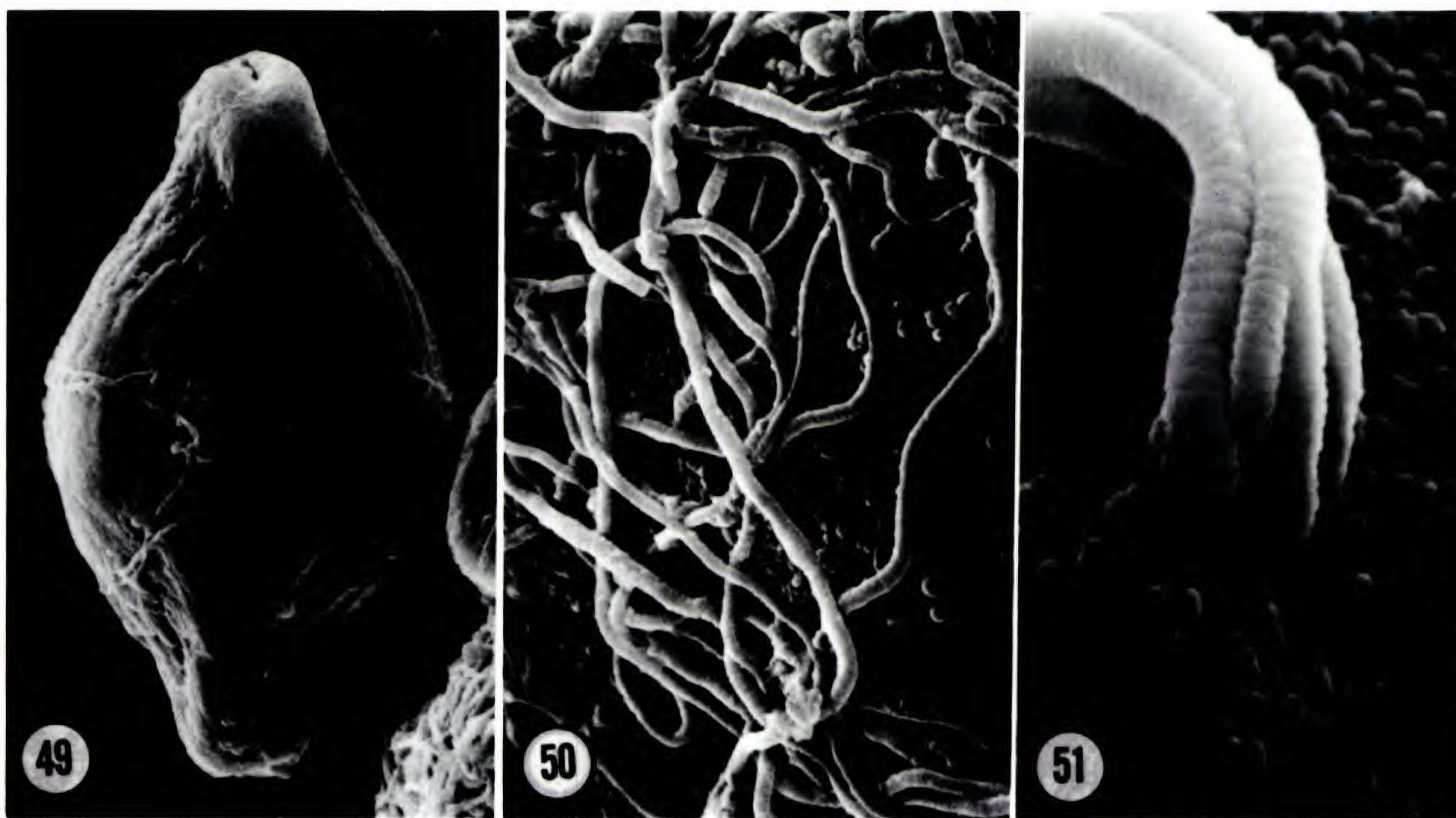
The unusual ultrastructure of Onagraceae has been analyzed and documented

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FIGURES 42–48. Nectary types in *Fuchsia* sects. *Fuchsia* and *Hemsleyella*.—42–47. Sect. *Fuchsia*.—48. Sect. *Hemsleyella*.—42–46, 48. Longitudinal sections.—47. Cross-section through the floral tube above the nectary, viewed from above.—42. Unlobed ring, *F. denticulata*, Berry 3065 (MO).—



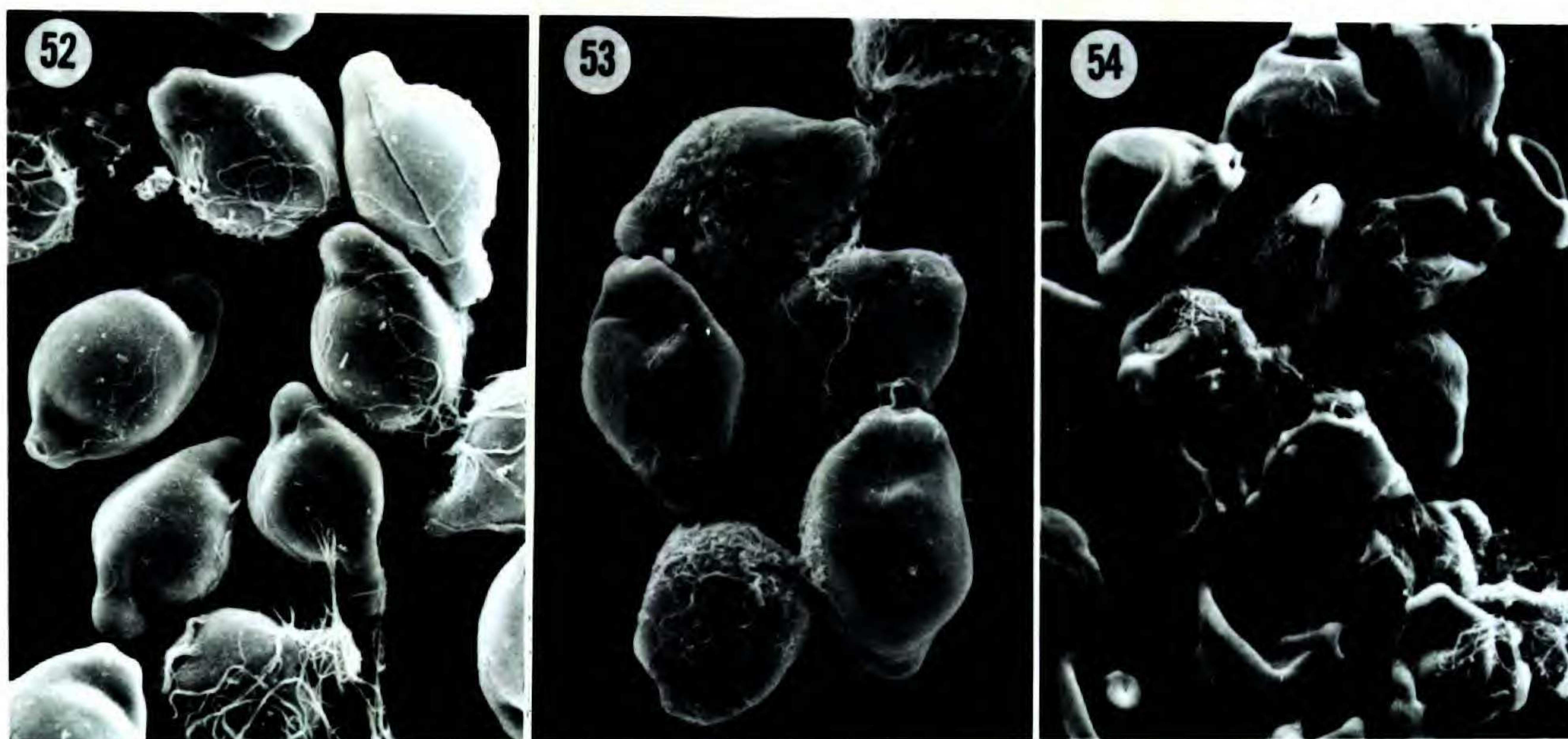
43. Four-lobed ring, *F. boliviana*, Berry 2592 (MO).—44. Irregularly lobed, adnate nectary of *F. pringsheimii*, Berry et al. 3709 (MO).—45. Nectary of *F. magdalenae*, J. O. Wright (pickled material, MO), consisting of nectariferous tissue lining the floral tube with 4 poorly defined prolongations. Note general similarity to the nectaries of sect. *Hemsleyella* (see Fig. 48).—46, 47. Separate, antesepalous lobes of *F. verrucosa*, Berry 3662 (MO). Style removed in Figure 46.—48. Smooth band nectary lining the base of the floral tube, *F. juntasensis*, Berry 3638 (MO); this type of nectary is characteristic of sects. *Hemsleyella*, *Ellobium*, and *Skinnera*.



FIGURES 49–51. SEM of pollen from *Fuchsia* sect. *Fuchsia*. (Provided by Joan W. Nowicke.)—49–50. *F. pilosa*, Berry 3618 (MO).—49. Whole grain, equatorial view (?), $\times 1,550$.—50. Surface of exine with viscin threads, $\times 5,000$.—51. *F. putumayensis*, Berry 3562 (MO), viscin thread attachment, $\times 15,000$. Note beaded thread type.

in a series of publications by J. J. Skvarla and coworkers (Skvarla et al., 1975, 1976, 1978). The taxa illustrated in the nine plates by Skvarla et al. (1976) include 17 of the then recognized 18 genera and are representative of the family. In most dicotyledons, the exine is stratified and consists of an ectexine that includes tectum, columellae, and foot layer, and an endexine. In most Onagraceae pollen, however, the exine is distinctly bizonal in thin section, and consists of an external spongy layer and an internal solid one. The spongy layer is now considered to represent the ectexine and it may be more or less homogeneous as in almost all species of *Fuchsia*, or it may be coarsely granular on the proximal face, e.g., as found in *Gongylocarpus* (Skvarla et al., 1976: Plate 3F), or the ectexine may be differentiated into a tectum and columellae, with the latter being uniform in size and distribution, e.g., as in *Camissonia arenaria* (Skvarla and Nowicke, unpublished data). The inner solid layer is now considered to be the endexine and is remarkably similar in all taxa examined in thin section (Skvarla et al., 1976; Nowicke and Skvarla, pers. comm.).

In *Fuchsia* (Figs. 49–54) the mature pollen is shed in monads, the grains are paraisopolar or heteropolar, and two-aperturate and bilaterally symmetrical (Figs. 49, 52, 53) or more rarely three-aperturate and radially symmetrical (Fig. 54). They are very large, and longest dimensions of $100\ \mu\text{m}$ are not uncommon. The apertures are compound and protruding, the ectoaperture is porate or slightly elliptical (elongated horizontally), the endoaperture consists of a circular oval-shaped opening in the endexine, and the massive deposition around this opening makes the endoaperture very conspicuous in light microscopy. The sculpture of the ectexine surface consists of globular elements, ovoid elements, or more rarely elongated



FIGURES 52–54. SEM of pollen from *Fuchsia* sect. *Fuchsia*. (Provided by Joan W. Nowicke.)—52. *F. putumayensis*, Berry 3562 (MO), grain at center left illustrates the expanded distal pole or face, the prominent “ridge” visible on a number of grains reflects the deposition of the endexine, $\times 500$.—53. *F. loxensis*, Berry 3185 (MO), views of grains at bottom right and center left are probably that of the distal pole but grains are partially collapsed, $\times 500$.—54. *F. vulcanica*, Berry 3190 (MO), almost all grains in this micrograph are 3-aperturate, but the sample included 2-aperturate ones also, $\times 350$.

elements. The viscin threads are mostly segmented-beaded or segmented-spiral, or more rarely smooth.

The vast majority of the Onagraceae, 590 of 675 species, have pollen with three apertures. However, in *Fuchsia*, 86 of 100 species have pollen with two apertures and in this respect the genus is unique within the family and a rarity in the dicotyledons. All species of the polyploid sections *Quelus* and *Kierschlegeria* have three-aperturate pollen. However, the separation of two-aperturate pollen from three is by no means absolute. In sect. *Fuchsia*, known polyploid populations of *F. vulcanica* and *F. corollata* show varying proportions of two and three-aperturate pollen grains. In a sample of the polyploid species *F. pringsheimii* there were a few grains with three apertures, but the apertures were not equidistant from each other. The remaining three tetraploid species in sect. *Fuchsia*, *F. triphylla*, *F. verrucosa*, and *F. magdaleneae*, were entirely two-aperturate. In addition, a number of species known only as diploids, such as *F. nigricans* and *F. venusta*, have a small proportion of three-aperturate grains (see Brown, 1967). Although increase in aperture number often accompanies polyploidy (see above for sect. *Quelus*, and Mosquin, 1966, for *Epilobium*), and this correlation clearly applies to sect. *Fuchsia*. It has been suggested for other onagraceous genera such as *Clarkia* that the occurrence of normal pore numbers in certain polyploid species and higher numbers in other polyploid species can be associated with older vs. more recent polyploidy (P. Raven, pers. comm.)

Since a majority of the species of *Fuchsia* have segmented threads, including all of the generalized South American sections, *Fuchsia*, *Hemsleyella*, and *Quelus*, as well as the early disjunct sect. *Skinnera*, this type of thread can be

TABLE 9. The distribution of viscin thread type, pollen pore number, and ploidy level in *Fuchsia*.

Section	Viscin Thread Type ¹	Pore Number	Gametic Chromosome Number
<i>Quelusia</i>	Compressed beaded	3	22, 44
<i>Fuchsia</i>	Compressed beaded	2, 3	11, 22
<i>Hemsleyella</i>	Compressed beaded	2, 3	11, 22
<i>Ellobium</i>	Compressed beaded	2	11
<i>Kierschlegeria</i>	Smooth	3	22
<i>Schufia</i>	Smooth	2	11
<i>Jimenezia</i>	Smooth	2	11
<i>Encliandra</i>	Smooth, ropy, and transitional smooth to beaded	2	11
<i>Skinnera</i>	Loosely beaded	2	11

¹ From Skvarla et al., 1978; Nowicke et al., in prep.

assumed to be primitive in *Fuchsia*. Smooth threads were found in the three probably derived Mexican and Central American sections, *Encliandra*, *Jimenezia*, and *Schufia*, as well as in the monotypic, anomalous sect. *Kierschlegeria* from coastal Chile. A general correlation found by Skvarla et al. (1978) was that segmented threads are associated with bird or moth pollination, whereas smooth, simple threads are associated with bee pollination. In *Fuchsia*, the sections with large hummingbird-pollinated flowers all have segmented threads, while all those with smooth threads have small flowers and may have at least some degree of insect pollination.

The pollen of species in sect. *Fuchsia* is remarkably similar and for that reason has limited taxonomic value. A summary of the distribution of viscin thread types, pore number, and ploidy level is presented in Table 9.

SYSTEMATIC TREATMENT

Taxonomic history of Fuchsia sect. Fuchsia. The earliest publication of *Fuchsia* was the description and illustration of “*Fuchsia triphylla flore coccineo*” by Charles Plumier in his *Plantarum Americanarum Genera* (1703). This species was found by the French missionary and naturalist during a stay in Haiti from 1689 to 1697 and was dedicated to Leonhart Fuchs, an important sixteenth century herbalist. The generic name *Fuchsia* was validated by Linnaeus (1737, 1753), using Plumier’s plate as the type of *Fuchsia triphylla* L.

The first group of South American species of sect. *Fuchsia* was discovered in Peru by the Spanish explorers Hipólito Ruiz and José Pavón between 1778 and 1788. They subsequently described six new species in the section (Ruiz & Pavón, 1802). A similar surge of collections and new species resulted from the explorations of Alexander von Humboldt and Aimé Bonpland in the northern Andes from 1800 to 1802. Five new species were described from their collections in a later publication (Humboldt et al., 1823).

As a result of the great horticultural interest that fuchsias generated in Europe in the early to mid-1800s, a large number of new discoveries were made in South

America. The biggest contribution came from specimens collected by Theodor Hartweg in Colombia and Ecuador in 1841 to 1843. In a series of fascicles begun in 1839 and called *Plantae Hartwegianae*, George Bentham described 12 new species of *Fuchsia*, 8 of which are currently recognized in sect. *Fuchsia*. Andrew Mathews made a set of valuable collections from northern Peru between 1830 and 1841, but no complete sets of his collections have been maintained. Fielding and Gardner (1844) described 2 species from Mathews' collections at Oxford, and Macbride (1940) found more extensive specimens at Geneva, from which he described 3 more species. Édouard André (1888) later followed much the same route in South America as Hartweg and managed to find several more novelties in sect. *Fuchsia*.

In the 20th century, Johnston (1925, 1939) and Macbride (1940, 1941) reviewed contemporary collections, mostly of A. Weberbauer from Peru, A. S. Hitchcock from Ecuador, and Macbride's own Peruvian collections, describing between them 26 new species in sect. *Fuchsia*. Only 11 of these names are currently recognized, however, which reflects the lack of a comprehensive understanding of the group by these authors. Regional floristic treatments of sect. *Fuchsia* have been made for Peru (Macbride, 1941) and for Ecuador (Munz, 1974). Philip Munz's (1943) generic revision of *Fuchsia* was the only attempt to examine the entire genus taxonomically at a sectional and specific level. Munz described nine new species in sect. *Fuchsia*, and a total of 100 species in 7 sections were recognized in the genus. Unfortunately, Munz's inability to examine critical material from European herbaria because of the outbreak of World War II and his lack of field experience and understanding of South American geography limited the thoroughness of his work.

Since Munz's monograph, collections of sect. *Fuchsia* have been enriched by important collectors such as José Cuatrecasas, John Wurdack, Ramón Ferreyra, César Vargas, and Julian Steyermark, as well as by a large number of other botanists including the author. The result of these collections has been a better geographical coverage of the areas in which *Fuchsia* occurs and a substantial increase in the number of specimens available, which has enabled us to redefine species limits and ranges in many taxa of the genus.

Fuchsia Linnaeus, Sp. Pl. 1191. 1753. TYPE: *Fuchsia triphylla* L.

Thilco Adanson, Fam. 2:498. 1763. TYPE: *Thilco* Feuillée, J. Obs. Phys. Math. Bot. Amér. Mérid. 3:64, pl. 47. 1725. "Thilco" or "Chilco" is the common name in Chile for *Fuchsia magellanica* Lamarck, and there is no doubt that this is what Feuillée illustrated and described.

Skinnera J. R. & J. G. A. Forster, Charact. Gen. 57. 1771. TYPE: *S. excorticata* J. R. & J. G. A. Forster = *Fuchsia excorticata* (J. R. & J. G. A. Forster) Linnaeus f.

Quelusia Vandelli, Fl. Lusit. Brasil. 23, fig. 10. 1788. LECTOTYPE: *Q. regia* Vandelli ex Vellozo = *Fuchsia regia* (Vandelli) Munz. Vandelli published the genus without naming a species. Munz (1943) designated *Fuchsia magellanica* as the lectotype, but that species occurs in Chile and Argentina, and Vandelli's publication was limited to Brazil. The illustration and description in Vandelli's book are in good agreement with *F. regia*.

Nahusia Schneevogt, Icon. Pl. Rar. 1:21. 1792. TYPE: *N. coccinea* (Aiton) Schneevogt = *Fuchsia coccinea* Aiton.

Thilcum Molina, Saggio Chili, ed. 2:146, 286. 1810. TYPE: *T. tinctorium* Molina = *Fuchsia magellanica* Lamarck.

Brebissonia Spach, Hist. Nat. Vég. Phan. 4:401. 1835, nom. rejic. TYPE: *B. microphylla* (Humboldt, Bonpland & Kunth) Spach = *Fuchsia microphylla* Humboldt, Bonpland & Kunth.

- Kierschlegeria* Spach, Hist. Nat. Vég. Phan. 4:403. 1835. TYPE: *K. lycioides* (Andrews) Spach = *Fuchsia lycioides* Andrews.
- Lyciopsis* Spach, Ann. Sci. Nat. Bot., sér. 2. 4:176. 1835. TYPE: *L. thymifolia* (Humboldt, Bonpland & Kunth) Spach = *Fuchsia thymifolia* Humboldt, Bonpland & Kunth.
- Schufia* Spach, Hist. Nat. Vég. Phan. 4:411. 1835. TYPE: *S. arborescens* (Sims) Spach = *Fuchsia arborescens* Sims.
- Encliandra* Zuccarini, Abh. Math. Phys. Cl. Königl. Bayer. Akad. Wiss. 2:335. 1837. TYPE: *E. parviflora* Zuccarini = *Fuchsia encliandra* Steudel.
- Kirschlegeria* H. G. L. Reichenbach, Handb. 246. 1837, orth. var. = *Kierschlegeria* Spach.
- Myrinia* Lilja, Fl. Sver. Suppl. 1:25. 1840, nom. rejic. TYPE: *M. microphylla* (Humboldt, Bonpland & Kunth) Lilja = *Fuchsia microphylla* Humboldt, Bonpland & Kunth.
- Spachia* Lilja, Tidning Trädgådsskötsel allmän Wextkultur 8:62. 1840, nom. illeg., non *Spachea* Jus-sieu. 1838. TYPE: *S. fulgens* (DeCandolle) Lilja = *Fuchsia fulgens* DeCandolle.
- Ellobium* Lilja, Linnaea 15:262. 1841, non *Ellobium* Blume. 1826, nom. rejic. Based on *Spachia* Lilja. 1840.
- Quilusa* J. D. Hooker, J. Linn. Soc., Bot. 10:460. 1869, orth. var. = *Quelusius* Vandelli 1788.

Erect to scandent shrubs, epiphytes, small- to medium-sized trees or procumbent creepers. Stems swollen or with tuberous underground parts in some species. Leaves simple, alternate, opposite, or whorled, with small, generally deciduous stipules. Flowers hermaphroditic, gynodioecious, or dioecious; actinomorphic, pedicellate, axillary or in racemose, paniculate, or involucrate inflorescences. Floral tube cylindric to obconic, deciduous in fruit. Sepals 4, valvate. Petals 4 or 0, convolute or spreading at anthesis. Stamens 8, biseriate, the antesealous ones usually longer than the antepetalous ones, all erect or the antepetalous ones reflexed and included in the floral tube. Anthers oblong to reniform, bilocular, dorsifixed, longitudinally and introrsely dehiscent. Pollen shed singly, 2–4 porate, with beaded to smooth viscin threads. Nectary present at the base of the floral tube. Ovary 4-locular, ovules ca. 8–400, (uni-) bi- to multiseriate. Stigma usually exserted, capitate, globose, or clavate, 4-lobed or subentire. Fruit a berry; seeds 6–ca. 400 per fruit, triangular to compressed in cross-section, obovoid to ellipsoid or irregularly triangular in outline. Basic chromosome number $x = 11$; gametic chromosome numbers $n = 11, 22$, and 44 .

Distribution (Figs. 1 and 2): Mostly cool, montane habitats in the Andes from Tierra del Fuego (55°S) to northern Colombia and Venezuela; in Central America and Mexico from central Panama to just north of the Tropic of Cancer (23°30'N); the coastal mountains of SE Brazil. Two species in Hispaniola, one species in central, coastal Chile; three species in New Zealand; one species in Tahiti. In the southern tip of South America and in coastal Chile, species descend to sea level.

The genus consists of nine sections, as outlined with their respective numbers and geographical ranges in Table 2. The following systematic treatment covers the main Andean section, sect. *Fuchsia*.

Fuchsia sect. **Fuchsia**

- Fuchsia* sect. *Quelusius* (Vandelli) DeCandolle, sensu DeCandolle, Prodr. 3:36. 1828, pro parte.
- Fuchsia* b. *Fuchsia* Zuccarini ex Endlicher, Gen. Pl. 1193. 1840.
- Fuchsia* sect. *Fuchsia* Zuccarini ex Walpers, Repert. Bot. Syst. 2:94. 1843.
- Fuchsia* sect. *Eufuchsia* Baillon, Hist. Pl. 6:467. 1877. Munz, Proc. Calif. Acad. Sci. IV. 25:15. 1943, pro parte.
- Fuchsia* sect. *Fuchsia*; Munz, N. Am. Flora II. 5:4. 1965, pro parte.

Erect, scandent, or climbing shrubs, subshrubs, or small trees. Leaves op-

posite or whorled. Flowers hermaphroditic, brightly (usually reddish) colored, divergent to pendant, axillary or arranged in racemose, paniculate, or involucrate inflorescences. Floral tubes longer than the sepals (except in *F. verrucosa*). Petals present and well developed, usually more than one-half as long as the sepals. Stamens erect, shorter than the sepals or slightly exerted beyond them. Nectary annular and mostly free from the floral tube, unlobed or shallowly 4–8-lobed, rarely an uneven band lining the base of the tube (in *F. magdalenae*) or composed of 4 or 8 prominent lobes adnate to the floral tube (in *F. pringsheimii* and *F. verrucosa*). Berry with ca. 50–250 seeds, the seeds compressed laterally and irregularly triangular-oblong in outline. Gametic chromosome numbers $n = 11, 22$.

Distribution (Figs. 1 and 2): Cloud forest of the tropical Andes from northern Argentina to Colombia and Venezuela; Hispaniola.

Unless otherwise indicated, measurements used in the key and species descriptions are based on dried herbarium specimens. In some characters such as floral tube thickness, stipule dimensions, and petal dimensions, this may represent a substantial reduction in size compared to living material, so certain compensation must be allowed when using living specimens. The key is almost entirely based on floral and foliar characters; since flowering and vegetative growth in sect. *Fuchsia* are essentially aseasonal, specimens are almost always collected with both leaves and flowers, so that lack of plant parts used in the key is rarely a problem. Floral tube length is measured from the top of the ovary to the rim of the tube, where the stamens and petals are inserted. Measurements of the antesepalous staminal filaments always precede those of the (shorter) antepetalous ones, and the number of secondary leaf veins always refers to the number of *each* side of the midvein.

The lack of major morphological differences and the overall similarity and variability in many species of sect. *Fuchsia* makes their separation by a simple key problematical, but a wide variety of characters are used when it is thought that the use of just one or two characters may be misleading. A number of dichotomies in the key are bridged by the variation present in certain species; in these cases, the species are keyed out under both entries.

Literature citations in the synonymy of each species are limited to the major floristic or revisionary treatments of the genus and to those references in which illustrations of the species are provided.

Since this paper covers a large number of taxa, some of them still poorly known, I have chosen not to recognize any taxa of subspecific rank. All the subspecific categories used by Munz (1943) were found to lie within the normal and continuous variation of their respective species. As with the other recent treatments in the family Onagraceae, considerably greater systematic knowledge of each species is required before subspecies are considered to be taxonomically meaningful units.

KEY TO THE SPECIES OF *FUCHSIA* SECT. *FUCHSIA*

- | | |
|---|----|
| 1a. Flowers axillary and subtended by normal or slightly reduced leaves, <i>not</i> tightly clustered at the branch tips, on short, lateral branches, or in definite inflorescences. | 2 |
| 1b. Flowers tightly clustered at the branch tips, in definite racemes, panicles, involucre, or on short, lateral, raceme-like branches. | 41 |

- 2a. Floral tube 3–32 mm long. ----- 3
- 2b. Floral tube 33–80 mm long. ----- 13
- 3a. Floral tube 3–6 mm long, shorter than the ovary. ----- (61) *F. verrucosa*
- 3b. Floral tube 10–32 mm long, longer than the ovary. ----- 4
- 4a. Floral tube obconic, 9–16 mm wide at the rim; sepals 18–25 mm long; Hispaniola. ----- (60) *F. pringsheimii*
- 4b. Floral tube cylindric to narrowly funnelform, 2–9 mm wide at the rim; sepals 6–17 mm long; South America. ----- 5
- 5a. Branching well-developed and strongly divaricate, with short tertiary branchlets; leaves 15–35(–45) mm long, 7–15 mm wide; secondary veins 4–6 on either side of the midvein; central to southern Peru. ----- (1) *F. decussata*
- 5b. Branching more or less lax and not strongly divaricate, short tertiary branchlets usually lacking; leaves generally more than 40 mm long, more than 15 mm wide; secondary veins 6–15 on either side of the midvein. ----- 6
- 6a. Leaves opposite, very rarely ternate, the blade conspicuously rugulose; stems, leaves, and flowers with stiff, white, hispid pubescence; flowers 2–6 per branch. ----- (6) *F. scabriuscula*
- 6b. Leaves not entirely opposite, whorls of 3 or 4 usually present. The blades not conspicuously rugulose; pubescence not hispid, or lacking; flowers generally 8 or more per branch. ----- 7
- 7a. Young stems and leaves glabrous or occasionally lightly pubescent, the leaves sometimes villous on the adaxial midrib. ----- 8
- 7b. Young stems and leaves canescent, strigose, or ferrugineous-pilose. ----- 9
- 8a. Leaves firmly membranous, elliptic to oblanceolate, the margin entirely or obscurely denticulate; petiole 5–25 mm long; flowers uniformly bright orange or scarlet; Peru and Bolivia. ----- (4) *F. sanctae-rosae*
- 8b. Leaves thinly membranous, elliptic-ovate, the margin gland-denticulate; petiole (15–)25–50 mm long; tube and sepals pale whitish-pink, the petals darker red to purple; Colombia and Ecuador. ----- (10) *F. pallescens*
- 9a. Pedicels 3–10 mm long; ovary and berry narrowly cylindric-fusiform, the berry 13–25 mm long; young growth densely canescent. ----- 10
- 9b. Pedicels (6–)8–32 mm long; ovary ellipsoid, the berry ellipsoid to subglobose, 9–18 mm long; young growth not densely canescent. ----- 11
- 10a. Leaves mostly finely reticulate or rugulose; floral tube narrowly funnelform, 3.5–7 mm wide at the rim; sepals 10–13 mm long; petals red; berry tapered towards the apex, 13–17 mm long, 5–7 mm thick; Ecuador. ----- (9) *F. sylvatica*
- 10b. Leaves not rugulose, mostly sulcate-veined; floral tube subcylindric, 3–6 mm wide at the rim; sepals 6–10 mm long; petals deep purple; berry barely tapered at the apex, 15–25 mm long, 5–10 mm thick; Colombia and Venezuela. ----- (8) *F. nigricans*
- 11a. Leaf margin obscurely denticulate; stems canescent to finely pilose, hairs not reddish; ovary strongly tetragonous; petals oblong-elliptic to subrotund, (2–)3–8 mm wide; Ecuador. ----- (5) *F. loxensis*
- 11b. Leaf margin distinctly denticulate or serrulate; stems mostly strigose-pilose, with white to reddish hairs; ovary terete or slightly angled; petals lanceolate to elliptic, 2–3 mm wide; Peru. ----- 12
- 12a. Basal leaves mostly quaternate and considerably larger than the upper ones, not bluish-tinged; secondary veins 8–14 on either side of the midvein; flowers grouped towards the branch tips and subtended by somewhat reduced leaves; flowers pink to red, the floral tube 4–6 mm wide at the rim; Dept. Amazonas (Peru). ----- (3) *F. fontinalis*
- 12b. Basal leaves mostly ternate and not much larger than the upper leaves, often bluish-tinged; secondary veins 6–10 on either side of the midvein; flowers subtended by normal leaves and not grouped at the branch tips; flowers red to blue violet, the floral tube usually 6–9 mm wide at the rim; Depts. San Martín to Junín (Peru). ----- (2) *F. ferreyrae*
- 13a. Leaves sessile or subsessile, the petioles 0.5–3 mm long. ----- 14
- 13b. Leaves not sessile or subsessile, the petioles more than 3 mm long. ----- 16
- 14a. Leaves 10–50 mm wide, the margin denticulate or serrulate, not revolute; stems glabrous to puberulent; Bolivia. ----- (37) *F. cochabambana*
- 14b. Leaves 2–6 mm wide, the margin subentire or revolute; stems ferrugineous-pilose; Ecuador and Peru. ----- 15

- 15a. Leaves elliptic-ovate, 8–12 mm long, 3–5 mm wide; pedicels 9–15 mm long; northern Peru. (33) *F. confertifolia*
- 15b. Leaves linear, 20–70 mm long, 2–3 mm wide; pedicels 16–20 mm long; southern Ecuador. (7) *F. steyermarkii*
- 16a. Petals broad, less than twice as long as wide, the apex rounded to broadly acute. 17
- 16b. Petals narrow, more than twice as long as broad, the apex narrowly to broadly acute. 28
- 17a. Sepals strongly reflexed soon after anthesis; petals erect; central Ecuador. (27) *F. ampliata*
- 17b. Sepals suberect to divergent, not strongly reflexed after anthesis; petals spreading to divergent. 18
- 18a. Leaves entirely opposite, generally (narrowly) ovate; southern Peru. (48) *F. vargasiana*
- 18b. Leaves not entirely opposite, whorls of 3 or 4 usually present, mostly not ovate. ... 19
- 19a. Secondary leaf veins mostly 3–8 on either side of the midvein. 20
- 19b. Secondary leaf veins mostly 8–22 on either side of the midvein. 24
- 20a. Petals usually longer than the sepals, rhombic to broadly elliptic, the base attenuate or unguiculate; leaves nitid on the upper surface, usually drying glossy and more or less bullate, margin markedly glandular-serrulate; southern Colombia to central Ecuador. (23) *F. corollata*
- 20b. Petals shorter or nearly equal to the sepals, not rhombic or with an attenuate or unguiculate base; leaves generally not drying glossy and bullate on the upper surface. 21
- 21a. Petals elliptic-ovate, usually markedly shorter than the sepals, 5–6(–9) mm wide; ovary terete or subterete, 5–6 mm long; leaf margin generally conspicuously gland-serrulate; floral tube pink cerise to purple lavender, often more or less strongly dilated near the middle; petals usually considerably darker than the sepals; southern Colombia. (24) *F. caucana*
- 21b. Petals orbicular to broadly elliptic-(ob-)ovate, only slightly shorter than the sepals, (6–)7–13 mm wide; ovary strongly tetragonous, 6–9 mm long; leaf margin subentire to gland-serrulate; floral tube orange to deep red, usually not strongly dilated near the middle; petals about the same color as the sepals. 22
- 22a. Leaves opposite or ternate, the margin gland-serrulate; pedicels 10–15 mm long; southern Ecuador. (36) *F. harlingii*
- 22b. Leaves 3–5-verticillate, margin subentire to denticulate; pedicels 5–55 mm long. 23
- 23a. Pedicels mostly somewhat tuberculate, 14–55 mm long; floral tube somewhat verrucose, 4–6 mm wide at the base, 10–12 mm wide at the rim, densely villous inside in the lower ¼–½; sepals thick-spongy, ca. 1.5 mm thick when fresh; petals usually drying purplish; berry 16–18 mm long, 8–11 mm thick; southern Peru to Bolivia. (35) *F. austromontana*
- 23b. Pedicels smooth, 5–25(–40)mm long; floral tube smooth, 3–4 mm wide at the base, 6–10 mm wide at the rim, pilose inside for most of the length; sepals membranous, less than 1 mm thick when fresh; petals not drying purplish; berry 11–15 mm long, 7–9 mm thick; southern Colombia and Ecuador. (26) *F. vulcanica*
- 24a. Floral tube 5–8 cm long, usually somewhat recurved; sepals 7–8 mm wide at the base; leaves mostly opposite, 6–27 cm long; Ecuador and Colombia. (38) *F. macrostigma*
- 24b. Floral tube 3.5–6 cm long, straight; sepals 3.5–7 mm wide at the base; leaves mostly in whorls of 3 or 4, 2–18 cm long. 25
- 25a. Young stems and leaves glabrous or very lightly strigose; nectary non-annular, a smooth band 3–6 mm high lining the base of the tube; northeastern Colombia. (39) *F. magdalenae*
- 25b. Young stems and leaves markedly pubescent; nectary annular, 1–3 mm high and mostly free from the base of the tube; southern Colombia to Bolivia. 26
- 26a. Petals 8–11 mm long, 5.5–8 mm wide, considerably smaller than the sepals; floral tube 5–8 mm wide at the rim; stems and leaves canescent-strigose to hirtellous with mostly appressed hairs; leaves 6–18 cm long, 2.2–7 cm wide. (25) *F. ayavacensis*
- 26b. Petals 12–17 mm long, 8–13 mm wide, nearly as long as the sepals; floral tube 8–12 mm wide at the rim; stems and leaves subglabrous to densely pubescent, the hairs usually more or less erect; leaves 2.5–8(–10) cm long, 1–4 cm wide. 27

- 27a. Leaves mostly glabrous on the upper surface; floral tube 4–6 mm wide at the base, somewhat tuberculate, the walls very firm and ca. 1.5 mm thick when fresh, the tube densely villous inside only in the lower $\frac{1}{4}$ – $\frac{1}{3}$; petals usually drying purplish; berry 16–18 mm long when ripe; southern Peru to Bolivia. (35) *F. austromontana*
- 27b. Leaves pubescent on the upper surface; floral tube 3–4 mm wide at the base, smooth, the walls not very firm, less than 1 mm thick when fresh, the tube pilose inside for most of its length; petals not drying purplish; berry 11–15 mm long; Ecuador. (26) *F. vulcanica*
- 28a. Leaf margin entire or more or less revolute, glandular teeth not visible without a lens. 29
- 28b. Leaf margin denticulate or serrate, glandular teeth clearly visible. 31
- 29a. Petals 9–11 mm long, smooth and not recurved; southern Ecuador. (32) *F. scherffiana*
- 29b. Petals 15–22 mm long, crispate-undulate and recurved when fresh. 30
- 30a. Secondary leaf veins 7–12 on either side of the midvein; leaves mostly ternate; sepal tips united in bud; Colombia and Venezuela. (28) *F. venusta*
- 30b. Secondary leaf veins 13–15 on either side of the midvein; leaves mostly quaternate; sepal tips mostly free and spreading in bud; northern Peru. (29) *F. rivularis*
- 31a. Leaves entirely opposite, generally (narrowly) ovate; northern Peru. (48) *F. Vargasiana*
- 31b. Leaves not strictly opposite, whorls of 3 or 4 usually present, not ovate. 32
- 32a. Petals about as long or longer than the sepals. 33
- 32b. Petals distinctly shorter than the sepals. 38
- 33a. Petiole 3–9 mm long. 34
- 33b. Petiole 10–40 mm long. 36
- 34a. Secondary leaf veins 3–8 on either side of the midvein; Colombia and Ecuador (23) *F. corollata*
- 34b. Secondary leaf veins 9–15 on either side of the midvein; northern Peru. 35
- 35a. Leaves ternate or mostly quaternate; secondary veins 13–15 on either side of the midvein; margin entire to denticulate; stems smooth. (29) *F. rivularis*
- 35b. Leaves opposite or ternate; secondary veins 9–13 on either side of the midvein; margin dentate; stems verrucose. (31) *F. llewelynii*
- 36a. Floral tube slightly striated-tuberculate, hirtellous, 3.5–5.5 mm wide at the base, 1–2 mm thick and firm-spongy when fresh, dull orange; pedicels 5–13 mm long; southern Colombia. (57) *F. canescens*
- 36b. Floral tube smooth, glabrous to strigose, 2.5–4 mm wide at the base, less than 1 mm thick and not firm-spongy when fresh, bright red to pink; pedicels 12–40 mm long. 37
- 37a. Petals elliptic to rhombic, (5–)6–10 mm wide; leaves firm, 2–7 cm long, 0.7–3 cm wide, usually drying more or less bullate and glossy on the upper surface; petioles 3–12(–22) mm long; southwestern Colombia and Ecuador. (23) *F. corollata*
- 37b. Petals elliptic-lanceolate to slightly obovate, 4–8 mm wide; leaves thin, 3.5–12 cm long, 1.5–5 cm wide, dull and not bullate when dry; petioles 10–48 mm long; Venezuela and northeastern Colombia. (30) *F. gehrigeri*
- 38a. Floral tube subcylindric, (3–)4–8 mm wide at the base, the walls very firm and 1–1.5 mm thick when fresh; ovary 10–13 mm long; anthers 4–6 mm long; Peru and Bolivia. (34) *F. denticulata*
- 38b. Floral tube funnelform 2–4(–6) mm wide at the base, the walls not very firm, less than 1 mm thick when fresh; ovary 5–8 mm long; anthers 2–4 mm long; Colombia and Ecuador. 39
- 39a. Young branches angled, densely cinereous-pubescent; leaves mostly quaternate; floral tubes 5–6(–8) mm wide at the rim; sepals 3–4 mm wide at the base; Colombia-Ecuador border area. (58) *F. cinerea*
- 39b. Young branches terete, not densely cinereous; leaves mostly ternate; floral tubes (4–)6–12 mm wide at the rim; sepals 5–9 mm wide at the base. 40
- 40a. Petals elliptic-ovate, 9–11(–14) mm long, obtuse to cuneate at the apex, glabrous, purplish and usually darker than the sepals; sepals 5–6 mm wide at the base; southern Colombia. (24) *F. caucana*
- 40b. Petals lanceolate to lance-elliptic, (8–)12–20 mm long, mostly acute at the apex, usually finely puberulent or villous on the dorsal surface, red and not much darker than the sepals; sepals mostly 6–9 mm wide at the base; central Colombia and Venezuela. (22) *F. petiolaris*
- 41a. Floral tubes 12–23 mm long. 42
- 41b. Floral tubes 24–130 mm long. 58

- 42a. Leaves sessile or subsessile, the petiole 0.5–5 mm long; secondary veins 18–25 on either side of the midvein. (44) *F. sessilifolia*
- 42b. Leaves not sessile or subsessile, the petiole more than 5 mm long; secondary veins 5–18 on either side of the midvein. 43
- 43a. Leaves entirely or mostly opposite. 44
- 43b. Leaves mostly 3–4-verticillate. 49
- 44a. Secondary leaf veins 3–8 on either side of the midvein; floral tube pale cream to pink, the petals much darker than the sepals. Ecuador and southern Colombia. (10) *F. pallescens*
- 44b. Secondary leaf veins 9 or more on either side of the midvein; floral tube red to orange, not pale or whitish, the petals not much darker than the tube and sepals. 45
- 45a. Stems and leaves densely pilose; leaves mostly ovate. 46
- 45b. Stems and leaves not densely pilose, subglabrous to puberulent or strigillose; leaves mostly elliptic, not ovate. 47
- 46a. Flowers in a compact, terminal raceme 1.5–7 cm long; pedicels 18–30 mm long; sepals 7–9 mm long; southern Peru. (46) *F. tinctoria*
- 46b. Flowers in axillary racemes or panicles 5–10 cm long; pedicels 10–20 mm long; sepals 10–13 mm long; Central Peru. (15) *F. ovalis*
- 47a. Flowers in axillary racemes or on short side branches, the subtending leaves not strongly reduced or modified; Peru. (13) *F. macrophylla*
- 47b. Flowers in terminal racemes with strongly reduced, subsessile, linear to lanceolate bracts; Colombia and Ecuador. 48
- 48a. Racemes generally elongate, 5–16 cm long, the bracts persistent; pedicels 3–7(–12) mm long, usually not divergent; sepals 6–8 mm long; secondary leaf veins 12–17 on either side of the midvein. (11) *F. orientalis*
- 48b. Racemes generally compact, 1–4(–10) cm long, the bracts mostly deciduous; pedicels divergent, 8–25 mm long; sepals 8–11 mm long; secondary leaf veins 9–13 on either side of the midvein. (17) *F. putumayensis*
- 49a. Pedicels 2–10 mm long. 50
- 49b. Pedicels 10–40 mm long. 54
- 50a. Leaves mostly in whorls of 4; flowers generally paniculate or densely crowded on the ultimate branches; berries subglobose, 6–10 mm long. 51
- 50b. Leaves mostly in whorls of 3; flowers racemose, few racemes on each plant; berries oblong to cylindrical, 13–25 mm long. 52
- 51a. Leaves 4 or more per whorl, the margin slightly denticulate; stems canescent to hirtellous; floral tube 13–20(–24) mm long, 1.5–3 mm wide at the base; Colombia. (55) *F. hartwegii*
- 51b. Leaves 4 or less per whorl, the margin markedly denticulate to serrate; stems canescent to densely pilose; floral tube 15–28 mm long, 3–4 mm wide at the base; northern Peru. (3) *F. fontinalis*
- 52a. Stems, leaves, and flowers densely pilose-hirsute; ovary 5–6 mm long; bracts narrowly lanceolate; northern Peru. (16) *F. pilosa*
- 52b. Stems, leaves, and flowers usually canescent or strigillose, never pilose or hirsute; ovary (6–)7–11 mm long; bracts ovate to elliptic; Venezuela to Ecuador. 53
- 53a. Leaves usually finely reticulate or rugulose; floral tube narrowly funnelform, 3.5–7 mm wide at the rim; sepals 10–13 mm long; petals red; berries tapered towards the apex, 13–17 mm long, 5–7 mm thick; Ecuador. (9) *F. sylvatica*
- 53b. Leaves not finely reticulate or rugulose; floral tube subcylindric, 3–6 mm wide at the rim; sepals 6–10 mm long; petals dark purple; berries barely tapered at the apex, 15–25 mm long, 5–10 mm thick; Colombia and Venezuela. (8) *F. nigricans*
- 54a. Leaves and branchlets glabrous or finely puberulent, except for hairs sometimes on the adaxial leaf midvein. 55
- 54b. Leaves and branchlets canescent to hirtellous or densely pilose. 56
- 55a. Flowers red, in axillary racemes or on short, lateral branches; leaves 5–9 cm wide; secondary veins 14–19 on either side of the midvein; central Peru. (13) *F. macrophylla*
- 55b. Flowers orange red, generally axillary, not in axillary racemes or on short side branches; leaves 1–4 cm wide, secondary veins 6–15 on either side of the midvein; southern Peru to Bolivia. (4) *F. sanctae-rosae*
- 56a. Leaves broadly elliptic to ovate; flowers in axillary racemes or panicles; central Peru. (15) *F. ovalis*
- 56b. Leaves lanceolate to elliptic, not ovate; flowers in terminal racemes or panicles. 57

- 57a. Leaves 4 or more per whorl, the margin slightly denticulate; stems canescent to hirtellous; floral tube 13–20(–24) mm long, 1.5–3 mm wide at the base; Colombia. (55) *F. hartwegii*
- 57b. Leaves 4 or less per whorl, the margin markedly denticulate to serrate; stems canescent to densely pilose; floral tube 15–28 mm long, 3–4 mm wide at the base; northern Peru. (3) *F. fontinalis*
- 58a. Leaves sessile or subsessile, petioles 0.5–3 mm long. 59
- 58b. Leaves not sessile or subsessile, petioles more than 3 mm long. 62
- 59a. Leaves 8–12 mm long, 3–5 mm wide; stems pilose; northern Peru. (33) *F. confertifolia*
- 59b. Leaves 30–120 mm long, 10–50 mm wide; stems glabrous or sparsely puberulent. 60
- 60a. Secondary leaf veins 4–5 on either side of the midvein; central Peru. (42) *F. coriacifolia*
- 60b. Secondary leaf veins 8–26 on either side of the midvein. 61
- 61a. Leaves 10–24 cm long, 4–8 cm wide, the margin entire; Ecuador and northern Peru. (12) *F. glaberrima*
- 61b. Leaves 3–6 cm long, 1–5 cm wide, the margin denticulate or serrate; Bolivia. (37) *F. cochabambana*
- 62a. Leaves entirely or mostly opposite. 63
- 62b. Leaves mostly in whorls of 3 or more. 81
- 63a. Floral tube 9–13 cm long; flowers in involucre with concave, sessile bracts; central Peru. (41) *F. ceracea*
- 63b. Floral tube less than 9 cm long; flowers not involucre with sessile, concave bracts. 64
- 64a. Flowers in axillary racemes or on short, lateral branches. 65
- 64b. Flowers in terminal racemes or panicles, not in axillary racemes or short, lateral branches. 66
- 65a. Floral tube 19–25 mm long; sepals 8–9 mm long, green-tipped; berry subglobose, 10–13 mm long, 8–9 mm thick. (13) *F. macrophylla*
- 65b. Floral tube 32–45 mm long; sepals 10–13 mm long, red; berry ellipsoid, 15–17 mm long, 7–10 mm thick. (14) *F. macropetala*
- 66a. Rachis elongate, 10–60 cm long. 67
- 66b. Rachis compact, 0.5–10 cm long. 70
- 67a. Secondary leaf veins 15–22 on either side of the midvein. 68
- 67b. Secondary leaf veins 8–14 on either side of the midvein. 69
- 68a. Petioles 4–10 mm long; sepals divergent after anthesis. (21) *F. abrupta*
- 68b. Petioles 20–70 mm long; sepals strongly reflexed after anthesis. (49) *F. boliviana*
- 69a. Leaves generally strigillose, 2.5–10(–13) cm long, 1–5 cm wide; floral tubes generally dilated near the middle and slightly constricted at the rim; petals 6–9 mm long; Hispaniola. (59) *F. triphylla*
- 69b. Leaves soft pilose, 7–18 cm long, 2–8 cm wide; floral tubes narrowly funnelform, not strongly dilated near the middle or constricted at the apex; petals 11–20 mm long; northern Peru. (51) *F. wurdackii*
- 70a. Secondary leaf veins mostly 3–7 on either side of the midvein; floral tube and sepals pale pink, petals purple. (10) *F. pallescens*
- 70b. Secondary leaf veins mostly 7–22 on either side of the midvein; floral tube and sepals not pale pink, petals not purple. 71
- 71a. Stems and leaves glabrous, puberulent, or velutinous. 72
- 71b. Stems and leaves coarsely pubescent (pilose, tomentose, or hispidulous). 79
- 72a. Floral tube 40–70 mm long. 73
- 72b. Floral tube 32–40 mm long. 74
- 73a. Leaves glossy, glabrous on the upper surface; secondary veins 8–12 on either side of the midvein; stems subglabrous; Colombia. (20) *F. cuatrecasasii*
- 73b. Leaves not glossy, usually strigillose or velutinous on the upper surface; secondary veins 13–17 on either side of the midvein; stems generally puberulent; central Peru. (50) *F. corymbiflora*
- 74a. Racemes (4–)5–15 cm long, suberect to nodding; leaves strigillose to subpilose; Hispaniola. (59) *F. triphylla*
- 74b. Racemes 2–5(–10) cm long, divergent to pendant, not suberect; leaves glabrous to puberulent; South America. 75
- 75a. Leaves oblanceolate, 10–24 cm long, 4–8 cm wide, often purple-flushed below; petioles stout, 3–8 mm long; ovary 7–9 mm long; stipules thick, persistent; Ecuador and northern Peru. (12) *F. glaberrima*
- 75b. Leaves mostly elliptic, 4–17 cm long, 2–10 cm wide, usually not purple-flushed below;

- petioles not stout, 4–30 mm long; ovary 2.5–7 mm long; stipules not thick and persistent. 76
- 76a. Petals 4–6 mm wide; ovary 4–7 mm long; floral tube (28–)35–40 mm long; southern Colombia. (20) *F. cuatrecasasii*
- 76b. Petals 2.5–4 mm wide; ovary 2.5–4 mm long; floral tube 23–35(–40) mm long; northern Peru to southern Colombia. 77
- 77a. Leaves elliptic to obovate, 2–10 cm wide, mostly opposite; sepals lanceolate, 3–5 mm wide. 78
- 77b. Leaves narrowly elliptic to narrowly (ob-)lanceolate, 1–4 cm wide, whorls of 3 or 4 usually present; sepals narrowly lanceolate, 2.5–4 mm wide; southern Ecuador. (18) *F. lehmannii*
- 78a. Branchlets finely puberulent; secondary leaf veins 9–13 on either side of the midvein; petioles 6–15 mm long; floral tube 15–27 mm long; southern Colombia to central Ecuador. (17) *F. putumayensis*
- 78b. Branchlets mostly strigillose; secondary leaf veins (8–)12–15 on either side of the midvein; petioles 6–30 mm long; floral tube 23–40 mm long; southern Ecuador and northern Peru. (19) *F. andrei*
- 79a. Ovary narrowly cylindric, 10–11 mm long; berry narrowly cylindric-fusiform, often more or less curved or with a strongly narrowed apex, 25–32 mm long; secondary leaf veins 12–18 on either side of the midvein; southern Peru. (48) *F. vargasiana*
- 79b. Ovary oblong, 5–10 mm long; berry oblong to globose, 12–20 mm long, not curved or with a strongly narrowed apex; secondary leaf veins 7–14 on either side of the midvein. 80
- 80a. Rachis 4–18 cm long; pedicels 9–11(–25) mm long; petals 9–16 mm long; leaf margin subdenticulate; stipules conspicuous, 3–5 mm long; northern Peru. (51) *F. wurdackii*
- 80b. Rachis 1.5–5 cm long; pedicels 15–40 mm long; petals 6–10 mm long; leaf margin denticulate or serrulate; stipules 2–3 mm long; Bolivia. (47) *F. furfuracea*
- 81a. Flowers in involucre with sessile, concave bracts. 82
- 81b. Flowers not in involucre with sessile, concave bracts. 83
- 82a. Floral tube 4–5 cm long; petals 9–13 mm long. (40) *F. simplicicaulis*
- 82b. Floral tube 9–13 cm long; petals 5–7 mm long. (41) *F. ceracea*
- 83a. Floral tubes 23–30 mm long. 84
- 83b. Floral tubes 30–76 mm long. 87
- 84a. Petioles (15–)25–50 mm long, secondary leaf veins 5–7(–9) on either side of the midvein; tube and sepals pale pink-cream, the petals much darker and purple. (10) *F. pallescens*
- 84b. Petioles 4–20(–25) mm long; secondary leaf veins 7–14 on either side of the midvein; tube and sepals not pale pink-cream, the petals not purple or much darker than the sepals. 85
- 85a. Young stems and leaves mostly pilose; leaf margin conspicuously gland-denticulate or serrulate; floral tube widest at the rim, where 4–6 mm wide; northern Peru. (3) *F. fontinalis*
- 85b. Young stems and leaves glabrous to strigose; leaf margin entire to finely denticulate; floral tube usually widest below the rim, 6–11 mm wide at the rim. 86
- 86a. Flowers densely crowded on short, divergent to pendant racemes 0.5–3 cm long; petals narrowly lance-oblong, 2.5–4 mm wide; southern Ecuador. (18) *F. lehmannii*
- 86b. Flowers generally not densely crowded, racemes suberect to nodding and 4–15 cm long; petals elliptic-ovate, 4–6 mm wide; Hispaniola. (59) *F. triphylla*
- 87a. Leaves entirely or mostly in whorls of 4 or more. 88
- 87b. Leaves entirely or mostly in whorls of 3. 93
- 88a. Petioles 12–35 mm long. 89
- 88b. Petioles 3–10(–15) mm long. 91
- 89a. Sepals 14–18 mm long, 6–9 mm wide at the base, thick-spongy and somewhat verrucose when fresh; petals trowel-shaped, 14–19 mm long, 4–7 mm wide; southern Colombia. (57) *F. canescens*
- 89b. Sepals 11–14 mm long, 3–6 mm wide at the base, not thick-spongy or verrucose when fresh; petals narrowly lanceolate to narrowly elliptic-oblong, 11–16(–18) mm long, 3–5(–6) mm wide. 90
- 90a. Young branches and leaves densely canescent to strigillose; leaves rarely more than 4 per whorl; stipules deciduous, not thick-callose when fresh, 1.5–2 mm long, 0.4–0.5 mm wide; southern Colombia and Ecuador. (53) *F. dependens*

- 90b. Young branches and leaves sparsely strigillose to strigose; leaves often more than 4 leaves per whorl; stipules thick-callose when fresh, persistent and recurved at the older nodes, 2.5–4 mm long, ca. 3 mm wide; central Colombia. ----- (56) *F. crassistipula*
- 91a. Flowers subracemose, not in panicles; pedicels 10–53 mm long; northern Peru. ----- (29) *F. rivularis*
- 91b. Flowers in panicles; pedicels 4–12 mm long. ----- 92
- 92a. Young stems and leaves hirtellous to strigillose; central Colombia. -- (54) *F. hirtella*
- 92b. Young stems and leaves finely puberulent to subglabrous; Ecuador and southern-most Colombia. ----- (45) *F. polyantha*
- 93a. Secondary leaf veins 15–25 on either side of the midvein. ----- 94
- 93b. Secondary leaf veins 7–15 on either side of the midvein. ----- 95
- 94a. Petioles 4–10 mm long; sepals not reflexed after anthesis; pedicels divergent to ascending. ----- (21) *F. abrupta*
- 94b. Petioles 20–70 mm long; sepals strongly reflexed after anthesis; pedicels pendant. ----- (49) *F. boliviana*
- 95a. Petals distinctly shorter than the sepals. ----- 96
- 95b. Petals nearly as long or longer than the sepals. ----- 98
- 96a. Floral tube 55–76 mm long; central Peru. ----- (43) *F. sanmartina*
- 96b. Floral tube 22–40 mm long. ----- 97
- 97a. Flowers tightly grouped in a raceme 0.5–3 cm long; petals 2.5–4 mm wide; southern Ecuador. ----- (18) *F. lehmannii*
- 97b. Flowers not tightly grouped, racemes 4–15 cm long; petals 4–6 mm wide; Hispaniola. ----- (59) *F. triphylla*
- 98a. Petioles 10–48 mm long. ----- 99
- 98b. Petioles mostly 2–10 mm long. ----- 100
- 99a. Pedicels generally short, 9–11(–25) mm long; ovary cylindrical, 7–10 mm long; leaves soft pilose, 7–18 cm long; stipules pale, 3–5 mm long and persistent; northern Peru. ----- (51) *F. wurdackii*
- 99b. Pedicels 12–40 mm long; ovary ovoid, often constricted near the apex, 5–7 mm long; leaves membranous, subglabrous to strigillose, 3.5–12 cm long; stipules dark, 1.5–2 mm long, often deciduous; Venezuela. ----- (30) *F. gehrigeri*
- 100a. Leaves mostly in whorls of 4, secondary veins 13–15 on either side of the margin; sepal tips usually free and spreading in bud; anthers narrowly oblong, 4–4.5 mm long; northern Peru. ----- (29) *F. rivularis*
- 100b. Leaves mostly in whorls of 3; secondary veins 7–12 on either side of the midvein; sepal tips usually connate in bud; anthers oblong, 2–3.5 mm long. ----- 101
- 101a. Young stems and leaves densely pilose, often with reddish hairs; leaves narrowly elliptic to oblanceolate, often somewhat curved to one side; not glossy; northern Peru. ----- (52) *F. mathewsii*
- 101b. Young stems and leaves subglabrous to finely hirtellous, never with reddish hairs; leaves elliptic, symmetrical, glossy on both sides; Colombia and Venezuela. ----- (28) *F. venusta*

1. ***Fuchsia decussata*** Ruiz & Pavón, Fl. Peruv. Chil. 3:88, pl. 323, fig. b. 1802. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):552. 1941, pro parte. Munz, Proc. Calif. Acad. Sci. IV. 25:56, pl. 8, fig. 44. 1943, pro parte. TYPE: Peru, Dept. Huánuco, abundant at Muña, 1778–1788, *Hipólito Ruiz & José Pavón* (MA, lectotype, here designated; photograph, MO). There are five Ruiz and Pavón collections of this species at MA, four at BM, and one each at F, G, MO, and NY. Since there is no collection data on any of the sheets, it is not possible to determine which sheets may be duplicates, so no islectotypes have been designated.

Fuchsia scandens K. Krause, Repert. Spec. Nov. Regni Veg. 1:171. 1905. TYPE: Peru, Dept. Huánuco, mountains SW of Monzón, 3,400–3,500 m, 1904–1920, *August Weberbauer* 3324 (B, holotype, destroyed in World War II; photograph, F). The photograph shows a poor specimen with few leaves or flowers and branches covered with lichens. Though this entity might correspond to *F. ferreyrae*, its leaves are closer to those of *F. decussata*, which the description does not exclude.

Fuchsia fusca K. Krause, Bot. Jahrb. Syst. 37:599. 1906. TYPE: Peru, Dept. Cuzco, Prov. La Convención, below Yanamanche, near road from Cuzco to Santa Ana, 3,300–3,400 m, 1904–1920, August Weberbauer 4975 (B, holotype, destroyed in World War II; photograph, F; G, isotype).

Suberect to scandent shrubs 1–3 m tall with a well-developed system of lateral, divaricate, often horizontal branches. Secondary and tertiary branches numerous, 2–4 per node and held at near 90° to stem, densely ferrugineous-tomentose to canescent; older stems 5–14 mm thick with sublustrous, copper red bark exfoliating in long, uneven strips. Leaves opposite or mostly ternate, firmly membranous, lanceolate to elliptic-obovate, acute to attenuate at the base, acute at the apex, 15–35(–45) mm long, 7–15 mm wide, usually dark green and subglabrous to strigillose above with impressed veins, paler below with strigose, usually reddish hairs along the veins; secondary veins 4–6 on either side of the midvein, subelevated below, higher order veins not visible without magnification, margin subentire to serrulate or denticulate. Petiole 3–10(–14) mm long, canescent to tomentose. Stipules filiform, 2–3 mm long, ca. 0.3 mm wide, mostly deciduous. Flowers axillary and few to numerous towards the tips of branches. Pedicels slender, strigose, at times slightly verrucose, arching-pendant, 15–25 mm long. Ovary oblong, 2–3 mm long, 1–1.5 mm thick. Floral tube subcylindric, 10–20(–23) mm long, 3–4 mm wide at the base, usually slightly narrowed to 2.5–3 mm wide above the nectary and slightly widened above to 4–6 mm wide at the rim, subglabrous to strigillose and occasionally verrucose outside, densely villous inside in lower ½–⅓. Sepals narrowly lanceolate, 8–10(–18) mm long, 2–3(–4) mm wide, narrowly acute at the apex, not much wider than the tube in bud, spreading at anthesis. Tube red to dark red, sepals red with dull green tips in bud. Petals scarlet to orange red, linear to broadly elliptic-ovate and often variable on the same plant, 5–9(–14) mm long, 1.5–4(–8) mm wide, apex acute. Nectary unlobed to obscurely 4-lobed, 1–1.5 mm high. Filaments red, 8–10 mm and 5–8 mm long; anthers oblong, 2–2.3 mm long, 1.2–1.5 mm wide, dull white. Style glabrous, red; stigma clavate to capitate, ca. 2 mm long and 1–2 mm wide, obscurely 4-cleft, white, exserted 4–8 mm beyond the anthers. Berry subglobose, subtetragonous before maturity, 8–9 mm long, 5–6 mm thick, red; seeds tan, 1.5–1.6 mm long, 0.8–1.0 mm wide.

Distribution: Peru. Scattered to locally frequent shrubs in thickets from tree line to mid-elevation cloud forest, from San Martín to Cuzco Depts., 2,900–3,400 m (Fig. 55).

Representative specimens examined: PERU, AYACUCHO: 19 km E of Tambo, *Berry* 3049 (MO, USM); 40–46 km NNE of Tambo, *Luteyn & Lebrón-Luteyn* 6352 (MO, NY); near Cusimachay, 25 km NE of Tambo, *Madison* 10374-70 (MO); Sigsiga, between Tambo and Ayna, *Tovar* 6148 (USM). CUZCO: Km 157 of Cuzco-Quillabamba road, *Berry* 2574 (CUZ, MO); Km 158 of Cuzco-Quillabamba road, *Berry & Aronson* 3041 (MO, USM); between Yanamanche and Quellomayo, *Vargas* 4512 (BH, CUZ, MO). HUÁNUCO: between Acomayo and Chinchao, *Ambrose et al.* 2397 (BH); 3 km E of Carpish tunnel, *Berry & Aronson* 3086 (MO, USM); Carpish, *Ferreya* 2093 (F, MO, NY, US, USM); Carpish, above Acomayo, *Hutchison & Wright* 5944 (F, G, LE, MICH, MO, NY, P, RSA, UC, US, USM); Muña, *Pearce* 513 (K); Tumanga, *Woytkowski* 7984 (US). JUNÍN: 64 km above Satipo to Concepción, *Berry & Aronson* 3075 (MO, USM). SAN MARTÍN: valley of Río Apisoncho, ca. 30 km above Jucusbamba, *Hamilton & Holligan* 552 (K, S, UC), 1057 (K), 1093 (K, UC).

Fuchsia decussata is distinguished from other members of its species group

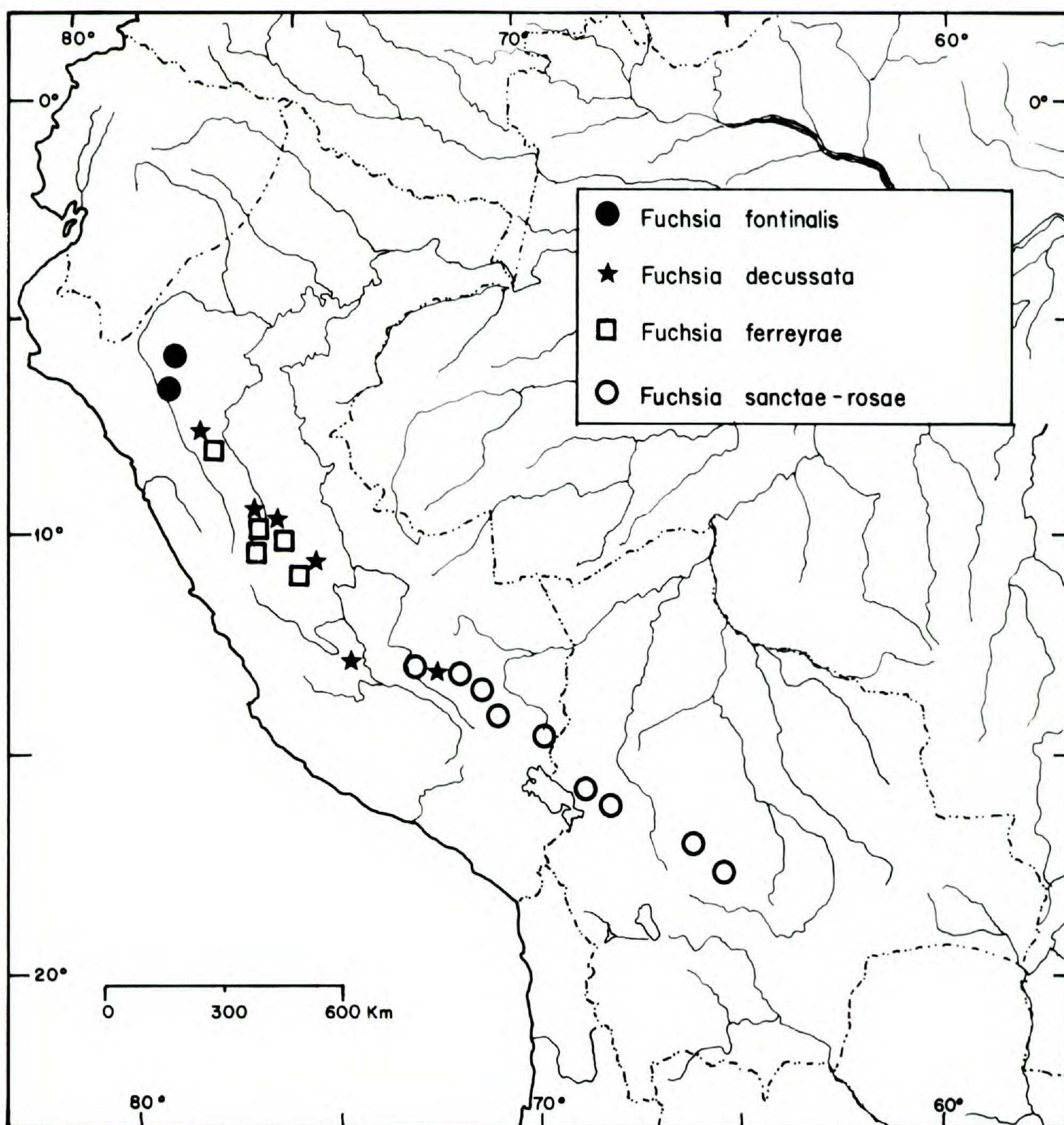


FIGURE 55. Distribution of the *Fuchsia decussata* species group.

by the small leaves with few secondary veins and the strongly divaricate branching pattern with short tertiary branchlets. It is closely allied to *F. ferreyrae*, and some intergradation between them may occur (see discussion under *F. ferreyrae*). It occurs sympatrically with *F. abrupta*, *F. corymbiflora*, *F. denticulata*, *F. ferreyrae*, and *F. sanmartina*.

Pubescence and petal size and shape vary considerably throughout the range of this species. Plants from the Carpish area in Huánuco have very narrow petals nearly as long as the sepals and a soft, reddish tomentum on the branches. Plants from Cuzco, such as the one described as *F. fusca*, have stiffer, more erect hairs, somewhat broader floral tubes, and wider petals. Extreme petal variation is found locally or in individual plants in Dept. Ayacucho. *Luteyn & Lebrón-Luteyn* 6352 (MO, NY) has petals 14 mm long and 8 mm wide, while the petals of *Berry* 3149

(MO, USM) from the same area vary widely, at times approaching the narrowly lanceolate petals of the Huánuco populations.

Sandeman 4585 (K, OXF; Dept. Junín, above Huacapistana, ca. 2,000 m, Oct. 1943) is a possible hybrid with *F. abrupta*. The flowers are subracemose with narrowly cylindric ovaries as in *F. abrupta*, but the short tubes (ca. 25 mm long) and branching system indicate parentage of *F. decussata*. Both species are known from the area, and less than 5% of the pollen of the presumed hybrid is stainable. Another collection from the same locality, *Sandeman 4503* (K) is more similar to *F. abrupta*, except that it has short floral tubes less than 25 mm long.

2. *Fuchsia ferreyrae* P. Berry, sp. nov. TYPE: Peru, Dept. Junín, Prov. Satipo, 68 km W of Satipo on road to Concepción, 3,110 m, 2 Aug. 1978, *Paul Berry & James Aronson 3073* (MO 2720583, holotype; MO, USM, isotypes). Named after Dr. Ramón Ferreyra, Director of the Museo de Historia Natural "Javier Prado" in Lima, Peru, and long-time collector of the Peruvian flora. Fig. 27.

Fuchsia decussata sensu Munz, Proc. Calif. Acad. Sci. IV. 25:56. 1943, pro parte.

Frutex erectus vel scandens 1–3 m altus, ramis arcuato-patentibus 0.5–1.5 m longis. Ramuli subcanescentes vel dense strigosi pilis interdum rubris instructi. Folia 3–4-verticillata vel raro opposita, membranacea, reticulata, elliptica vel obovata, basi acuta vel acuminata apice acuta, 2–8 cm longa, 1–3 cm lata, superne atroviridia subtiliter strigulosaque, subtus nervis praesertim strigosis et pagina saepe cyanescenti; nervis secundariis utroque latere 6–10, margine obscure vel valde glanduloso-serrulata; petiolis 4–12 mm longis; stipulis filiformibus, 2–4 mm longis, deciduis. Flores atroviridi vel atrovioleacei, axillares et numerosi ad apicem ramorum dispositi; pedicellis tenuibus dependentibusque, 12–30 mm longis. Tubi florales anguste infundibuliformes, (15–)22–28 mm longi, basi 3–4 mm lati et conspicue nodosi inde ca. 2 mm lati valde constricti, superne dilatati summo (6–)8–9 mm lati, extus strigulosi vel pilosi intus glabrati. Sepala anguste lanceolata, acuminata, (10–)14–16 mm longa, ca. 3 mm lata, alabastro saepe apicibus libris. Petala rubra vel violacea, elliptica, acuta, plerumque plus minusve dimidio breviora quam sepalis, 7–9 mm longa, ca. 3 mm lata. Filamenta antisepala 9–13 mm longa, antipetala 5–9 mm longa, antheris oblongis, ca. 2 mm longis ca. 1.5 mm latis. Stylus glaber, stigmatibus capitatis, apice leviter 4-fisso, ca. 2 mm longo latoque, obscure albido. Bacca ellipsoidea vel subglobosa, ca. 12 mm longa, ca. 8 mm lata, nitens purpureaque; seminibus 1–1.2 mm longis, ca. 0.6 mm latis. Numerus gameticus chromosomatum $n = 11$.

Erect to climbing-scandent shrubs 1–3 m tall with horizontally divergent to arcuate branches 0.5–1.5 m long. Branchlets subcanescent to coarsely strigose with reddish hairs; older branches with finely fissured, dull tan to coppery bark. Leaves in whorls of 3 or 4, occasionally opposite or subopposite, membranous, elliptic to obovate, acute to attenuate at the base, acute at the apex, 2–8 cm long, 1–3 cm wide, velvety dark green and strigillose above, strigose below especially along veins and often flushed with a bluish tinge; secondary veins 6–10 on either side of the midvein, higher order veins reticulate and usually visible without magnification; margin moderately to strongly glandular-serrulate. Petiole pubescent, 4–12 mm long. Stipules filiform, 2–4 mm long, ca. 0.4 mm wide, deciduous. Flowers axillary and numerous towards the branch tips. Pedicels slender, pendant, 12–30 mm long. Ovary oblong, ca. 3 mm long. Floral tube narrowly funnelform, (15–)22–28 mm long, 3–4 mm wide and conspicuously nodose at the base, then $\pm$ abruptly narrowed to ca. 2 mm wide above the nectary and gradually widened above until (6–)8–9 mm wide at the rim, strigillose to pilose outside, glabrous inside. Sepals narrowly lanceolate, (10–)14–16 mm long, ca. 3 mm wide, acuminate, often with free tips in bud, divergent at anthesis. Tube and sepals dark red to deep violet (blue red). Petals red to violet, elliptic, usually about half

as long as the sepals, 7–9 mm long, ca. 3 mm wide, acute at the apex. Nectary unlobed, ca. 1.5 mm high. Filaments red to violet, 9–13 mm and 5–9 mm long; anthers oblong, ca. 2 mm long, ca. 1.5 mm wide. Style glabrous, red to violet; stigma capitate, ca. 2 mm long and wide, slightly 4-lobed, dull white. Berry ellipsoid to subglobose, ca. 12 mm long, ca. 8 mm thick, lustrous purple; seeds 1–1.2 mm long, ca. 0.6 mm wide. Gametic chromosome number $n = 11$.

Distribution: Central Peru. Locally frequent shrubs in openings of cloud forest from San Martín to Junín Depts., 2,600–3,150 m (Fig. 55).

Specimens examined: PERU, HUÁNUCO: Pano, *Macbride* 3615 (G, GH, F, K, S, US); Tambo de Vaca, *Macbride* 4414 (F, GH); ca. 22 km SE of Huánuco, *Macbride & Featherstone* 2081 (F, G, GH, US), 2107 (F, GH, K, US), 2124 (F, GH); Pillao, *Woytkowski et al.* 34163 (F, MO, UC, USM). JUNÍN: 68 km W of Satipo to Concepción, *Berry & Aronson* 3074 (MO). SAN MARTÍN: valley of Río Apisoncho, ca. 30 km above Jucusbamba, *Hamilton & Holligan* 1428 (K, S, UC). WITHOUT LOCALITY: *McLean s.n.* (K).

This species is closely related to *Fuchsia decussata* but has more nodose, funnellform floral tubes, generally shorter petals, longer and more reticulate leaves, and less divaricate branching. Some plants, such as the type collection, have a very striking blue-violet coloration on the leaves and flowers (Fig. 27). This species lacks the green sepal tips of *F. decussata*. It occurs sympatrically with *F. abrupta*, *F. decussata*, *F. denticulata*, and *F. sanmartina*.

Around the type locality in Dept. Junín, *F. ferreyrae* is found between 2,650 and 3,100 m. At ca. 2,900 m, it is sympatric with *F. decussata*. Although these two species occur side by side, no intermediate plants could be found. In this area, the two species differ markedly in appearance. *Fuchsia decussata* has flaky, coppery bark and a tight, divaricate branching system with slender, green-tipped flowers. Plants of *F. ferreyrae* are much more floriferous, with broader, more nodose, and totally violet flowers and laxer, simpler branching. In many herbarium specimens, however, it is difficult to distinguish the two species because coloration and leaf texture characters are usually lost upon drying. Several of the specimens cited under *F. ferreyrae* are intermediate with *F. decussata* in certain characters, but are included here because of their noticeably nodose and funnel-form floral tubes, larger leaves, or indication of bluish coloration in the foliage. Additional field work is needed in Dept. Huánuco to determine if these species intergrade or if they are always clearly distinct under field conditions, as found at the type locality.

3. ***Fuchsia fontinalis*** J. F. Macbr., *Candollea* 8:25. 1940. TYPE: Peru, Dept. Amazonas, Chachapoyas, 1830–1841, *Andrew Mathews* (G-DEL, lectotype, here designated; photograph, MO).

Fuchsia decussata sensu Munz, *Proc. Calif. Acad. Sci.* IV. 25:56. 1943, pro parte.

Erect to scandent shrubs 0.5–4 m tall with spreading branches. Young growth canescent to densely pilose, often becoming ferrugineous with age; branchlets pilulose to tomentose; older branches 5–12 mm thick with tan, finely fissured bark. Leaves whorled, mostly ternate or quaternate, occasionally opposite, membranous, elliptic to (ob-)lanceolate, acute to attenuate at the base, acute at the apex, 35–110 mm long, 10–35 mm wide, strigillose above and along the veins below, basal leaves noticeably larger than the upper ones; undersurface visibly

reticulate-veined, secondary veins 8–14 on either side of the midvein; margin conspicuously denticulate or serrate. Petioles pubescent, 5–21 mm long, mostly reddish. Stipules filiform, 2–3 mm long, ca. 0.4 mm wide, deciduous to semipersistent. Flowers numerous and generally densely grouped in upper leaf axils or in racemes or many branched terminal panicles; rachis 3–14 cm long with reduced leaves 15–25 mm long subtending the flowers. Pedicels slender, pendant, pubescent, 6–16(–25) mm long. Floral tube subcylindric to narrowly funnelform, 15–28 mm long, 3–4 mm wide and somewhat bulbous at the base, then constricted to ca. 2 mm wide above the nectary and widened gradually above until 4–6 mm wide at the rim, pilose to strigillose outside, glabrous inside. Sepals lanceolate, 10–13 mm long, ca. 3 mm wide, acuminate, spreading-divergent at anthesis. Tube and sepals nitid red or pink. Petals red, usually noticeably shorter than the sepals, lanceolate, 6–9 mm long, 2–3 mm wide, acute, spreading at anthesis. Nectary 4–8-lobed, ca. 1.5 mm high. Filaments pink to red, 9–14 mm and 6–10 mm long; anthers oblong, 2–2.5 mm long, 1–1.5 mm wide, dull white. Style light red, glabrous; stigma capitate, slightly 4-lobed, 1.5–2 mm long and wide, exserted 2–4 mm beyond the anthers. Berry subglobose, 9–10 mm long, 5–9 mm thick, red; seeds tan, 1–1.2 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Shrubs in thickets, banks, and streamsides; endemic to Dept. Amazonas, in upper cloud forest on the E side of the Jalca de Calla-Calla and in the mountains to the east of the Río Utcubamba, 2,900–3,400 m (Fig. 55).

Representative specimens examined: PERU, AMAZONAS: Cerros de Calla-Calla, 18 km SW of Leimebamba (Km 403), *Ambrose 2375* (BH); E side of Calla-Calla, 62 km NE of Balsas, *Berry & Escobar 3608* (MO, USM); Cerro Puma-Urco, 10 km SE of Chachapoyas, *Berry & Escobar 3624* (MO, USM); Leimebamba-La Joya trail, *Boeke 1783* (MO); Leimebamba-Lajasbamba trail, *Boeke 2031* (MO); Cerros Calla-Calla, E side, 18 km above Leimebamba, *Hutchison & Wright 6956* (F, NY, RSA, UC, US, USM); Almirante, *Mathews 1479* (K, OXF); Chachapoyas, *Mathews s.n.* (G-BOIS); Cerro Tinaja, *Ochoa 1653* (F, US); mountains S of Tambo de Ventilla, *Pennell 15794* (PH); Almirante, *Sandeman 59* (F, OXF); upper slopes of Puma Urco, ESE of Chachapoyas, *Wurdack 670* (F, NY, RSA, US, USM); S side of Molinopampa-Diosán pass, *Wurdack 1626* (RSA, US, USM).

This species is allied to *F. decussata* and *F. ferreyrae*. Its flowers are more numerous, however, and are often grouped into definite inflorescences. The leaves are mostly quaternate, unlike the other two species, and the basal leaves are usually considerably larger than the upper leaves.

At its lower altitudinal limit on the eastern slopes of the Jalca de Calla-Calla, *F. fontinalis* is sympatric and forms local hybrids with *F. mathewsii* along pasture borders and stone walls (Fig. 10 and discussion under *F. mathewsii*).

4. ***Fuchsia sanctae-rosae*** Kuntze, Rev. Gen. 3(2):98. 1898. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):562. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:59, pl. 9, fig. 48. 1943. TYPE: Bolivia, Santa Rosa (Department unknown), 1,600 m, 13–20 April 1892, *Otto Kuntze* (NY, holotype). This specimen is in very poor shape, and no intact flowers remain, but the description and locality could only apply to this species.

Fuchsia boliviana Britton, Bull. Torrey Bot. Club 17:214. 1890, hom. illeg., non Carr., 1876. TYPE: Bolivia, Dept. La Paz, Yungas, 1885, *Henry H. Rusby 1813* (NY, holotype; MICH, NY, US, isotypes).

Fuchsia weberbaueri K. Krause, Repert. Spec. Nov. Regni Veg. 1:179. 1905. TYPE: Peru, Dept. Puno, Prov. Sandia, 2,400 m, 1906, *August Weberbauer 661* (B, holotype, destroyed in World War II; photograph, F; G, isotype).

Fuchsia brittonii Johnston, Contr. Gray Herb. 75:39. 1925, nom. nov. pro *F. boliviana* Britton, hom. illeg.

Fuchsia filipes Rusby, Mem. New York Bot. Gar. 7:317. 1927. TYPE: Bolivia, Dept. La Paz, Pulcheri, ca. 3,000 m, 15 July 1921, *Orland E. White 232* (NY, holotype; GH, K, US, isotypes; photographs of GH isotype, NY, RSA).

Erect to scandent, well branched shrubs 1–3 m tall. Branchlets usually subglabrous, occasionally pubescent, purplish red, 2–4 mm thick; older branches 5–18 mm thick with light tan, finely fissured bark. Leaves usually ternate or quaternate, the basal ones much larger than the upper ones, membranous, oblanceolate to (narrowly) elliptic, acute to attenuate at the base, acute to acuminate at the apex, 2–14 cm long, 1–4 cm wide, dark green and glabrous above, paler below (especially when dry) and glabrous except often with pilose hairs along the midrib; secondary veins 6–15 on either side of the midvein, subelevated below; margin subentire to obscurely denticulate. Petiole subglabrous to pubescent, 5–25 mm long, green to red-purple. Stipules lance-linear to narrowly triangular, occasionally connate, 2–4 mm long, 0.5–1.0 mm wide, deciduous. Flowers usually numerous, solitary in upper leaf axils or often appearing loosely racemose or paniculate. Pedicels slender, glabrous, 10–30(–40) mm long, spreading-divergent to drooping. Ovary cylindric, 4–5 mm long, 1–2.5 mm thick. Floral tube subcylindric to narrowly funnelform, 15–22(–27) mm long, 2–3 mm wide at the base, slightly constricted above the nectary and gradually widened above until 4–6 mm wide at the rim, glabrous to sparsely pilose outside, densely pilose inside in lower $\frac{1}{3}$. Sepals lance-oblong, acute, 9–13 mm long, 2.5–4 mm wide, rather obtuse-tipped in bud and broader by 1–2 mm than the rim of the tube, spreading-divergent at anthesis. Tube and sepals nitid orange red. Petals orange red, oblong, obtuse to acute, 7–9 mm long, 2–4 mm wide, spreading. Nectary unlobed, ca. 1.5 mm high. Filaments orange red, 6–8 mm and 4–6 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide, cream. Style orange red, glabrous; stigma orange red, capitate, slightly 4-lobed, ca. 1.5 mm long and wide, exerted 3–4 mm beyond the anthers. Berry ellipsoid to subglobose, 8–12 mm long, 6–10 mm thick, dark red purple; seeds 1.3–1.6 mm long and 0.8–1.0 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Peru and Bolivia. Scattered to locally frequent shrubs in cloud forest from Dept. Cuzco in Peru to Dept. Cochabamba in Bolivia; 1,400–3,000 m (Fig. 55).

Representative specimens examined: PERU, CUZCO: Machupichu, *Balls B6802* (BM, F, K, NA, UC, US); ca. 13 km below Marcapata to Quince Mil, *Berry & Aronson 3019* (MO); Km 170 of Cuzco-Quillabamba road, *Berry & Aronson 3046* (MO); Km 127–128 of Cuzco-Pilcopata road, *Berry et al. 2596* (MO, USM); Km 160 of Cuzco-Paucartambo-Pilcopata road, *Berry et al. 3002* (MO, USM); San Miguel, Urubamba valley, *Cook & Gilbert 1110* (GH, US); Hacienda Santa Rita, Urubamba valley, *Dreyfus s.n.* (USM); above Machupichu on old Inca trail, *Gentry et al. 19384* (MO); Amaybamba, Prov. Convención, *Infantes 6033* (P); Machupichu, *Mexia 8078* (F, G, GH, K, MO, UC); Pillahuata, Cerro de Cusilluyoc, *Pennell 13997* (F, GH, NY, PH, US); between Calca and Hipal, Quebrada de Yanatili, *Raimondi s.n.* (USM); Aguas Calientes, Urubamba valley, *Solomon 3118* (MO); between Pillahuata and Tambomayo, *Vargas 82* (BH, CAS, CUZ, F, MO); Huailai, Marcapata, *Vargas 1343* (CUZ); Km 75–76 road to Lares, *Vargas 15322* (CUZ); Mant'o, Km 84, *Vargas 15627* (CUZ); valley of Río Tambomayo, *West 7091* (GH, MO, UC). PUNO: Santo Domingo

area, Prov. Sandia, *McCarroll* 14 (MICH, NY, S); 2–6 km from Oconeque, Prov. Sandia, *Metcalf* 30557 (A, BH, G, MO, UC, US); Ollachea, Prov. Carabaya, *Vargas* 6869 (CUZ, RSA); vicinity of Sandia, *Vargas* 15151 (CUZ); San Juan de Oro, Prov. Sandia, *Vargas* 20604 (CUZ); Agualani-Oconeque, Prov. Sandia, *Vargas* 20635 (CUZ). BOLIVIA, COCHABAMBA: Montepunco, 130 km E of Cochabamba, *Adolfo* 314 (DS); Incachaca, *Brooke* 6693 (F, NY), 6653 (NY); road to Yungas de Tablas, *Cárdenas* 6259 (NY, US). LA PAZ: Chulumani, *Albert de Escobar* 1303 (TEX); El Chaco, Sur Yungas, *Asplund* 1153 (UPS); Unduavi, *Brooke* 6610 (BM, F, NY, U); Hacienda Simaco, road to Tipuani, *Buchtien* 832 (BM, F, G, K, MO, POM), 5508 (GH, NY, S, US, Z); between Unduavi and Chirca, *Eyerdam* 25388 (F, UC); from Puente Villa to Chulumani, *Kelley* 1014 (UC); near Ananca, Machacamarca, Prov. Larecaja, *Mandon* 624 (BM, F, G, GH, LE, NY, RSA, S, W); Rio Pelechuco, *Williams* 2494 (BM, NY); Nequejahuira, Cordillera Real, *Tate* 675 (NY); Okara, Cordillera Real, *Tate* 912 (NY).

This species can be distinguished from other axillary, short-flowered species by the nearly entire leaves, usually glabrous stems and leaves (except for the pilose midvein below), and the uniformly orange red, nitid flowers. In addition, the stigma is reddish, and the basal leaves are considerably larger than the upper ones. It occurs sympatrically with *F. cochabambana*, *F. boliviana*, *F. denticulata*, *F. furfuracea*, *F. tincta*, and *F. vargasiana*.

Fuchsia sanctae-rosae has uncommonly wide ecological and altitudinal tolerances. It is found in open, rocky situations such as the ruins of Machupichu or in shady cloud forest thickets. In Dept. Puno, Peru, it occurs on the edges of the town of Ollachea in ditches at 2,700 m; in the neighboring Dept. Cuzco, it occurs as low as 1,400 m, where subtropical floristic elements are already present (Fig. 11).

Beck 1266 (MO; Bolivia, Dept. La Paz, Prov. Murillo, Valley of Zongo at 2,170 m, 10 km from Cahua towards La Paz) is a probable hybrid with *F. denticulata*. This specimen has the stout stems and firm, elliptic leaves of *F. denticulata*, but the flowers are characteristic of *F. sanctae-rosae*, except for the intermediate tube length. The pollen stainability is 63% of 500 grains. Probable hybrids with *F. furfuracea* and *F. tincta* are discussed under those respective species.

5. *Fuchsia loxensis* Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 6:106, *t.* 536, *figs.* 1–5. 1823. Munz, Proc. Calif. Acad. Sci. IV. 25:28, *pl.* 2, *fig.* 14. 1943; Opera Bot., Ser. B, 3:18. 1974. TYPE: Ecuador, Prov. Loja, near Loja, ca. 2,000 m, July–Aug. 1802, *Alexander von Humboldt & Aimé Bonpland* (P HBK. Herb., holotype, not seen; photograph, F; microfiche, MO).

Fuchsia umbrosa Benth, Pl. Hartw. 176. 1845. TYPE: Ecuador, Prov. Pichincha, Hacienda de Pinantura, near Quito, 1841–1843, *Theodor Hartweg* 983 (K Benth. Herb., holotype; BM, BR, CGE 2 sheets, G, K Hooker Herb., LE, OXF, W, isotypes).

Fuchsia apiculata I. M. Johnston, Contr. Gray Herb. 75:34. 1925. TYPE: Ecuador, Prov. Azuay and Cañar, between Cuenca and Huigra, 2,700–3,300 m, 12–13 Sept. 1923, *Albert S. Hitchcock* 21667 (GH, holotype; photograph, UC; NY, US, isotypes).

Fuchsia hypoleuca I. M. Johnston, Contr. Gray Herb. 75:34. 1925. TYPE: Ecuador, Prov. Loja, between Loja and San Lucas, 2,100–2,600 m, 6 Sept. 1923, *Albert S. Hitchcock* 21440 (GH, holotype; photograph, UC; NY, US, isotypes). Munz, Proc. Calif. Acad. Sci. IV. 25:57, *pl.* 8, *fig.* 45. 1943; Opera Bot., Ser. B, 3:17. 1974.

Scandent to mostly erect shrubs or small trees (1–)1.5–6 m tall, usually densely branched. Young growth canescent to finely pilose; older stems 8–25(–40) mm thick, with flaky, tan bark. Leaves ternate or quaternate, membranous, (narrowly)

elliptic to oblanceolate, acute to narrowly cuneate or subrounded at the base, acute to acuminate at the apex, 2–9(–13) cm long, 0.8–3(–4) cm wide, medium to dark green and subglabrous to strigose above, pale green and strigose-pilose below, especially along the veins; secondary veins (5–)6–10(–13) on either side of the midvein; margin (sub-)denticulate. Petioles mostly strigose, 7–15(–17) mm long. Stipules narrowly lanceolate, 2–4 mm long, ca. 1 mm wide, subpersistent. Flowers few to numerous and solitary in leaf axils. Pedicels drooping, 8–23(–32) mm long. Ovary ellipsoid to cylindric, 5–8 mm long, 1.5–2.5 mm thick. Floral tube narrowly funnelform, (15–)19–30(–33) mm long, 2–3(–4) mm wide and slightly bulbous at the base, then narrowed to 1.5–2.5 mm above the nectary and gradually widened above until 5–8 mm wide at the rim, sparsely strigose outside, pilose in lower $\frac{1}{3}$ inside. Sepals ovate-lanceolate to lanceolate, 9–16 mm long, 3–5 mm wide, acute, spreading to strongly divergent or slightly reflexed at anthesis. Tube and sepals bright scarlet. Petals dull scarlet, oblong-elliptic to subrotund, 6–10(–11) mm long, (2–)3–8 mm wide, acute to rounded at the apex. Nectary mostly unlobed, ca. 1 mm high. Filaments red, 5–10 mm and 4–7 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide, white. Style red, pilose in lower $\frac{1}{2}$ – $\frac{1}{3}$; stigma capitate, 4-cleft at the apex, 1.5–2.5 mm long, 1–2.5 mm wide, cream to scarlet. Berry ellipsoid, 4-angled before maturity, 13–18 mm long, 7–10 mm thick, red purple when ripe; seeds 1.5–2 mm long, ca. 0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuadorian Andes. Locally common in hedgerows along fields and in thickets, mainly in the moderately dry interandean valleys of Ecuador, also on the moister eastern and western slopes, from Loja to Pichincha, with a few scattered collections farther north in Imbabura and Carchi, (2,000–)2,500–3,500(–3,800) m (Fig. 56).

Representative specimens examined: ECUADOR, AZUAY: 13 km from Cuenca past Sayausí, *Berry & Escobar 3185* (MO, QCA); along Río Yanucay above San Joaquín, *Berry & Escobar 3210* (MO); along Río Matadero W of Cuenca, *Camp E-1914* (NY, RSA, US); Sayausí, *Harling 1396* (NY, S); Tambo-lama and Huasi-huaico, W of Cuenca, *Lehmann 4595* (K). BOLIVAR: Chaparro de Gualicón, Loma, Cordillera Occidental, *Acosta Solis 6268* (F); Urcu-corral Chillanes, *Acosta Solis 6624* (F); Pucará de Telimbela, Cordillera Occidental, *Acosta Solis 6818* (F); Alto de Telimbela, *Acosta Solis 7154* (F); Balsapampa to San Miguel, *Harling et al. 9531* (RSA). CAÑAR: near Pimo, *Camp E-4135* G, MO, NY, P, RSA, S, UC, VEN); between Cuenca and Huigra, *Hitchcock 21688* (US); Ventanillas, above Shoray, E slope of Cerro Yanguang, 34 km ENE of Azogues, *Fosberg & Prieto 22775* (RSA, US); between Tambo and Sucsá, *Giler (Camp number) E-2756* (NY, RSA). CARCHI: Páramos de El Ángel, *Benoist 3637* (P). CHIMBORAZO: Sibambe, Hacienda La Carmela, sección Era-Pata, Cordillera Occidental, *Acosta Solis 5432* (F); road from Pusucucho to El Placer, Cordillera Oriental, *Acosta Solis 7253* (F); road from Chambo to Sanguay, *Albert de Escobar 1091* (TEX); near Quinacorral, *André in 1876* (K); slopes of Cerro Chiguazo, *Lugo 512* (RSA); Javiñac, ca. 15 km from Panipe, *Lugo 519* (RSA); ca. 3–4 km from Puela, *Lugo 576* (RSA); Chontapamba, between Puela and Baños, *Lugo 741* (RSA); Manzano, 1 km from Puela, *Lugo 1303* (RSA); between Baños and Riobamba, *Lugo 1844* (RSA); between Guaranda and Bodegas, *Remy in 1836* (P); vicinity of Huigra, Hacienda de Licay, *Rose 22477* (US); road Riobamba-Huamboya, *Scolnik 1533* (RSA); Pallatanga, *Spruce 5798* (BM, CGE, G, K 2 sheets, NY, OXF, TCD, W); Hacienda Joyagshi, road from Sibambe to Tambo, *Wiggins 10705* (POM). COTOPAXI: San Miguel, *André 4015* (K); Pilaló, *Harling 4877* (LL, NY, S); from Pilaló to Macuchi, *Haught 2955* (POM, US); Pilaló, *Holm-Nielsen & Jeppesen 1141* (AAU, S); Panamerican highway, ca. 6 km N of Lasso, ENE of Pastocalle, *Sparre 15805* (S). IMBABURA: Páramo de Cotacachi, from Otavalo to Apuela, *Davis 276* (MO); Mojanda, *Sodiño in 1903* (P). LOJA: Cisne, *André s.n.* (K); Loja, *André s.n.* (K); between Saraguro and San Lucas, *Asplund 17973* (NY, S); 5 km S of Saraguro, *Berry & Escobar 3192* (MO); 11 km S of Saraguro, *Berry & Escobar 3196* (MO); Cerro Villonaco, *Berry & Escobar 3204* (MO), *Camp E-238* (NY, RSA); Cerros de Acacana, ca. 30 km N of Loja,

Espinosa E-1440 (POM, RSA); mountains of Loja, *Hartweg 733* (BM, CGE, G, K, LE, NY, OXF, P, W); Km 43 on Panamerican highway N of Loja, *Holm-Nielsen 4708* (AAU, MO, NY, S); San Lucas, *Jameson 170* (K); Santiago, *Poortman 151* (P); Cerro Villonaco, 20 km W of Loja, *Sparre 16244* (S). PICHINCHA: Gualilagua, El Corazón, *Acosta Solis 7110* (F); Valle Seco del Pedregal, *Acosta Solis 8442* (F); near Tambillo, *André 3681* (K); Páramo de Paguangualli, Corazón, *André in 1876* (K); Machachi, *Asplund 6226* (S); Páramos de Aloag, *Benoist 3060* (P, RSA); N of Volcán Cotopaxi on Panamerican highway, *Berry & Escobar 3233* (MO, QCA); INIAP station, 14 km S of Quito, *Escobar 621* (MO); ascent to Cotopaxi, *Espinosa E-2342* (RSA); between Tambillo and Aloag, 28 km S of Quito, *Fosberg 22549* (COL, NY, RSA, US); road Quito to Santo Domingo de los Colorados, near top of cordillera, *Gentry 9470* (MO, S); vicinity of Tambillo, *Penland & Summers 959* (F, GH, POM, RSA); pass at Páramo el Corazón, *Prescott 922* (DS, NY); near Quito, *Sodiño in 1898* (P); road to Iliniza, *Sparre 15785* (S); Panamerican highway, ca. 1 km N of RR, ESE of El Chaupi, *Sparre 15801* (S). TUNGURAHUA: between Leito and La Cima, *Acosta Solis 9024* (F); between Huambaló and Cotaló, *Acosta Solis 9717* (F); between La Cima and Riochico, *Acosta Solis 10234* (F); Hacienda Yanayacu, Mocha, *Balls B7188* (F, K, UC, US); near Agua de Oro, W of Ambato, *Heinrichs 828* (G, NY, Z); Mocha, *Laudeman 35* (BM); Runtún, ca. 4 km from Baños, *Lugo 1190* (MO, RSA); Cusatagua, near Ambato, *Pachano 217* (NY, US); S of Baños, *Penland & Summers 93* (BH, F, POM); near Baños, *Spruce 5203* (BM, CGE, G, GH, K, LE, NY, OXF, P, TCD, W). ZAMORA-CHINCHIPE: Km 12–14 road from Loja to Zamora, *Dodson & Thien 1369* (DS, MO).

Fuchsia loxensis is distinguished from other axillary, short-flowered species in the following combination of characters: leaves ternate or quaternate, elliptic to subrotund petals, 4-angled ovaries, and a generally erect, shrubby to arborescent habit. Although it has been placed in its own species group with two other short-flowered, but rather distantly related species, the leaves and flower shape resemble some of the long-tubed members of the *F. petiolaris* species group such as *F. ampliata*. It occurs sympatrically with *F. ampliata*, *F. harlingii*, and *F. vulcanica*.

As treated here, *F. loxensis* is a wide ranging and variable species including all the short-tubed, strictly axillary-flowered collections of *Fuchsia* in Ecuador except for *F. scabriuscula* and *F. steyermarkii*. The shape of the leaves, petals, and floral tubes as well as pubescence are characters that vary widely in this complex. The plant habit and habitat are important characters that, unfortunately, are too little known for most collections because detailed field observations have not been made. Plants that I have seen in Pichincha and Azuay were large, erect shrubs with thick basal stems and often grew in hedgerows. Plants in northern Loja were more sprawling in thickets, as is more typical in the section. There are too few critical field observations in this group, and further study may lead to the recognition of additional taxa. Some of the different geographical variants found are:

The Central Valley in Pichincha, Cotopaxi, Tungurahua, and Azuay. Collections from these areas are from high elevations (over 3,200 m in the north and above 2,800 m in the south) and are generally from erect, hedgerow shrubs. The habitats in these areas are somewhat drier than most fuchsias tolerate. The type of *F. umbrosa* has rather long, ampliate floral tubes (31–33 mm long), sepals 16 mm long, and broad leaves, but it comes from the Central Valley southeast of Quito and may just be a robust shade plant of *F. loxensis*.

Imbabura. The two specimens from this province grow at high elevations (ca. 3,400 m) but have unusually short floral tubes (ca. 15 mm long), oblong petals, and thin, ternate leaves with narrowly cuneate to attenuate leaf bases. This might be a new or different species, but more material is needed.

Bolívar and western Cotopaxi. Collections from the western slopes of the

Andes in these provinces grow at considerably lower elevations (2,400–2,800 m) than the previous groups, and they often have larger leaves and flowers. No living plants of these entities were seen, and there might be some intergradation with *F. ampliata*.

Northern Loja. Local populations occurring between Saraguro and San Lucas have an unusual white leaf undersurface and until now have been recognized as a separate species, *F. hypoleuca*. As noted in the original publication of that species (Johnston, 1925) however, it is an associated fungus with a thick layer of whitish mycelia, not the plant's own pubescence, that causes the unusual leaf characteristic. In the mass of mycelia and epidermal trichomes that one finds together on the leaf undersides, stalked structures called "brown caps" by D. B. O. Savile (pers. comm.) are often observed, and anatomical sections show that these are definitely part of the fungus and not glandular processes of the plant epidermis (R. Keating, pers. comm.). Fungal specimens sent to a specialist for examination were apparently sterile and could not be identified (D. B. O. Savile, pers. comm.). Wider sampling of *Fuchsia* populations in Loja and further evaluation of this fungal relationship will be necessary before the relationships of these northern Loja populations with others of *F. loxensis* can be confirmed, however.

Tungurahua and Cañar. The set of collections labelled *Spruce 5203* probably is a mixture of *F. loxensis* (sheets at BM, CGE, NY, and OXF), while others (G, GH, and P) have nitid, dentate leaves and floral tubes ca. 35 mm long. The lack of any specific locality information makes evaluation of these specimens difficult.

Hitchcock 21667 (GH, NY, US), from the Azuay-Cañar border area, was described as *F. apiculata*, but its buds are no more pointed than other collections throughout the range of this complex, and no other distinguishing characters are apparent.

6. ***Fuchsia scabriuscula*** Bentham, Pl. Hartw. 177. 1845. Munz, Proc. Calif. Acad. Sci. IV. 25:58, pl. 8, fig. 46. 1943; Opera Bot., Ser. B, 3:22. 1974. TYPE: Ecuador, Prov. Pichincha, W slopes of the Quito Andes, Oct. 1843, *Theodor Hartweg* 987 (K Bentham Herb., holotype; photograph, MO; BM, BREM, CGE, G, K Hooker Herb., OXF, isotypes; photograph of B isotype, POM). Fig. 22.

Decumbent to erect shrubs 0.5–2.5 m tall. Branchlets subterete, 2–5 mm thick, pilose-hispidulous with suberect, whitish hairs; older branches with tan, exfoliating bark. Leaves opposite, very rarely ternate, membranous, with finely reticulate, rugulose venation, elliptic to slightly ovate, acute to rounded at the base, acute to acuminate at the apex, 2.5–12(–14) cm long, 1.5–5(–6) cm wide, dull green and strigose above, pale green to flushed purple and strigose below, especially along the veins; secondary veins 8–14 on either side of the midvein, subelevated below; margin subentire. Petioles densely pilose, 5–25 mm long. Stipules lance-linear, 2–3.5 mm long, thick at the base, terminating in a long, dark, filiform tip, subpersistent. Flowers few and solitary in upper leaf axils. Pedicels divergent to drooping, pilose, 10–25 mm long. Ovary oblong, 5–6 mm long, 2–3 mm thick, strigose to hispidulous, green. Floral tube narrowly funnel-

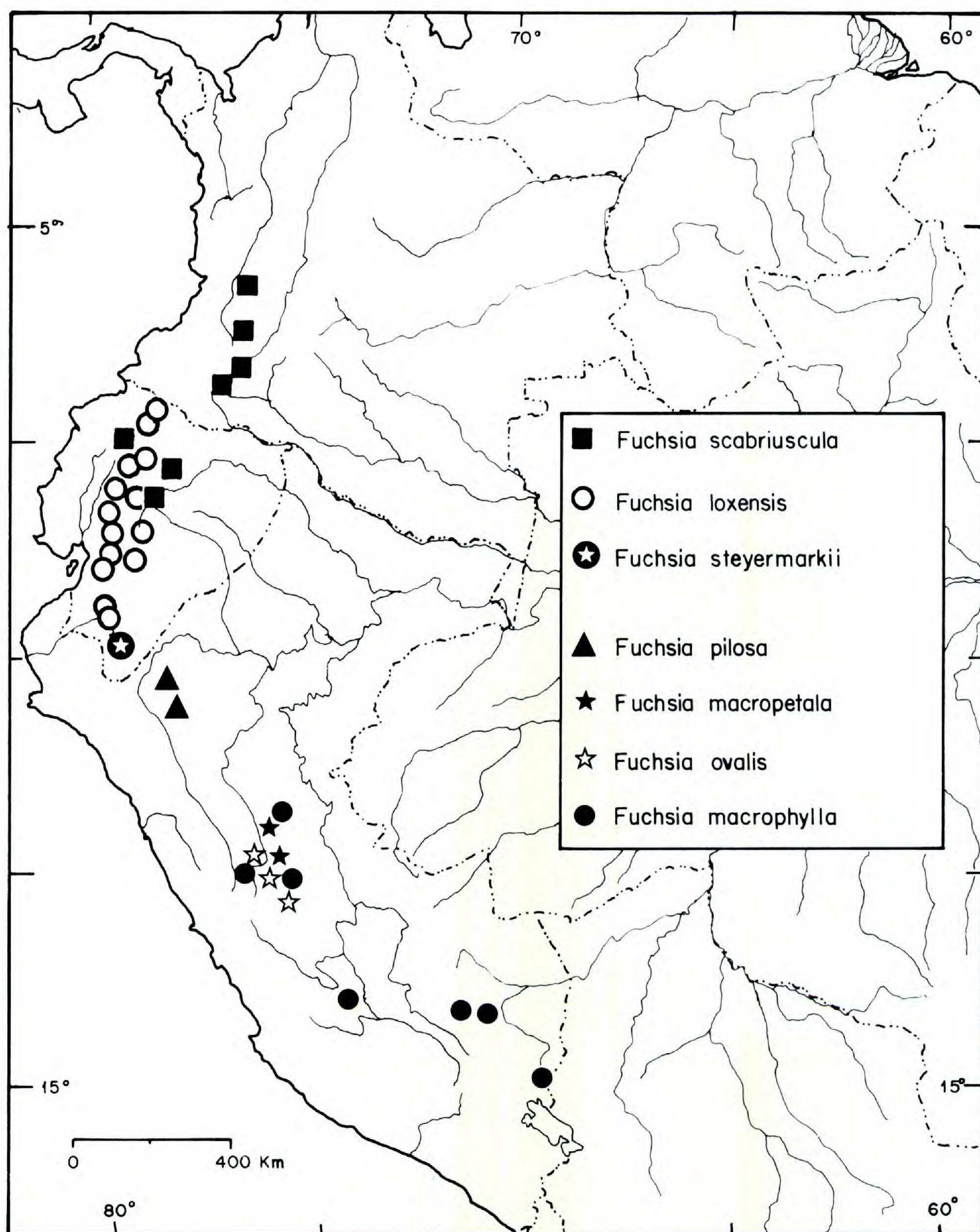


FIGURE 56. Distribution of the *Fuchsia loxensis* and *F. macrophylla* species groups.

form, 15–27 mm long, 2–3 mm wide at the base, slightly narrowed to 1.5–2.5 mm wide above the nectary and gradually widened above until 5–7 mm wide at the rim, strigose to hispidulous outside, densely pilose inside in lower $\frac{1}{2}$. Sepals lanceolate, 9–12 mm long, 3–4 mm wide, acuminate, tips mostly free in bud, spreading at anthesis. Tube and sepals whitish pink to red. Petals pink to scarlet, elliptic-oblong, 7–10 mm long, 3–4.5 mm wide, broadly acute to rounded at the apex, spreading at anthesis. Nectary usually unlobed, green, ca. 1.5 mm high.

Filaments red to pink, 5–7 mm and 3–5 mm long; anthers elliptic-oblong, 1.5–2 mm long, ca. 1 mm wide, bright white. Style densely villous for most its length, pink; stigma subglobose, 4-cleft at the apex, ca. 2 mm long and ca. 2 mm wide, exserted 1–4 mm beyond the anthers, white. Berry oblong before maturity, becoming subglobose when ripe, usually deep, nitid purple; seeds tan to bright purple, 1–1.3 mm long, 0.8–1.0 mm wide.

Distribution: Ecuador and southern Colombia. Low shrubs locally frequent in clearings, thickets, and moist banks of cloud forest; in Ecuador, in Napo, Pichincha, and Tungurahua Provinces, on both the east and west slopes of the Andes; in Colombia, on the eastern slopes of the Nudo de Pasto in Putumayo, in the Cordillera Central as far north as Valle, and in the Cordillera Oriental to the Cauca-Huila border; 1,400–2,750 m (Fig. 56).

Representative specimens examined: COLOMBIA, CAUCA: Km 31–32 from Pitalito toward Mocoa, *Berry* 3596 (COL, MO); Río Villalobos, vicinity of Río Suazita, *Schultes & Villarreal* 5173 (COL, F, GH). HUILA: Km 25 of Pitalito-Mocoa road, *Berry* 3593 (COL, MO); Km 28–32 of road from Pitalito to Mocoa, *Luteyn et al.* 7550 (COL, MO, NY); La Plata, *von Sneider* 2462 (S). PUTUMAYO: Mirador, between San Francisco and Mocoa, *Bristol* 545 (GH); Río Susunga, 18–20 km W of Mocoa, *Fosberg* 20395 (NY, RSA, UC, US); Km 90–91 between Sibundoy and Mocoa, *Luteyn et al.* 5041 (COL, MO); Los Monos, Km 92 between San Francisco and Mocoa, *Plowman & Davis* 4328 (COL). VALLE: El Guayabo, from Palmira to Taco, *Berry & Escobar* 3565 (COL, MO). ECUADOR, NAPO: Río Chingual, *Acosta Solis* 13250 (F); Cuyuja, *Balslev & Madsen* 10476 (AAU, MO); between Baeza and Papallacta, *Mexia* 7339 (GH, NA, S, UC, US); Baeza to Tena, ca. 5 km S of Cosanga, *Øllgaard & Balslev* 10248 (AAU, MO); above Baeza on road to Quito, *Plowman et al.* 3889 (COL, F, GH, K). PICHINCHA: Guaruna, Km 38 of road to Saloya, *Acosta Solis* 11018 (F); Mindo, *André* in 1876 (K); Corazón, towards Miligalli, *André* 3710 (K, NY); Salvador, below San Juan, *Asplund* 16184 (NY, S); 34 km W of Chillogallo towards Chiriboga, *Berry & Escobar* 3243 (MO, QCA); 30 km W of Cotacallao towards Nanegal, *Berry & Escobar* 3178 (MO, QCA); W slope Cerro Corazón, *Camp E-1663* (NY, RSA); Quito-Santo Domingo road, *Haught* 3224 (A, BH, US); Quito Andes, *Jameson* 92 (BM, G, GH, P); Quito-Nono-Puerto Quito road, 13 km NW of Nono, *Luteyn et al.* 6519 (MO, NY); road Nono-Tandayapi, Km 43–45 along Río Alambí, *Sparre* 15989 (S). TUNGURAHUA: Baños, *Benoist* 4223 (P); Río Verde, *Harling et al.* 10159 (MO, RSA); valley of Río Pastaza, between Baños and Cashurco, *Hitchcock* 21781 (GH, NY); Montaña Woma, 11 km E of Baños, *Holm-Nielsen & Jeppesen* 279 (AAU, DS); Volcán Tungurahua, *Lehmann* 4995 (F, K). WITHOUT LOCALITY: *Spruce* 5038 (BM, CGE, G 2 sheets, GH, F, K, LE, NY, OXF, S 2 sheets, TCD, W 3 sheets).

This species is easily distinguished by its finely rugulose, opposite leaves and stiff, whitish pubescence on most parts. Just a few flowers are borne on each branch; these later produce round, dark purple berries. *Fuchsia scabriuscula* occurs sympatrically with *F. cuatrecasasii*, *F. hartwegii*, *F. macrostigma*, *F. orientalis*, *F. pallescens*, *F. sessilifolia*, *F. sylvatica*, and *F. verrucosa*. No hybrids have been detected with these species, despite close examination of several populations.

7. *Fuchsia steyermarkii* P. Berry, sp. nov. TYPE: Ecuador, Prov. Zamora-Chinchiipe, between Rancho Achupallas and Tambo Valladolid, deep forest along the W side of Río Valladolid to Río Molino, 1,800–2,000 m, 12 Oct. 1943, *Julian A. Steyermark* 54596 (NY, holotype; photograph, MO).

Frutex pilosus ramosissimus ca. 2 m altus. Folia linearia, revoluta, opposita vel 3–4-verticillata sed plerumque fasciculata, firme membranacea ambis extremis acuta, 20–70 mm longa, 2–3 mm lata, superne subnitida atroviridia strigosaque, subtus pallidioria praesertim in costa media margineque dense pilosa; nervis secundariis plerumque inconspicuis, margine valde revoluta; petiolis 0.2–2.0 mm

longis; stipulis fuscatis, lanceolato-linearibus, ca. 1.5 mm longis, subpersistentibus. Flores pauci, axillares, ad apicem ramorum dispositi; pedicellis 16–18 mm longis; ovario oblongo, 4–5 mm longo. Tubi florales roseo-rubri, anguste infundibuliformes, 33–37 mm longi, basi 2.5–3 mm lati et bulbosi inde ca. 2 mm lati constricti superne gradatim dilatati summo 5–6 mm lati, extus laxe strigoso-pilosi, intus infra medium pilosi. Sepala lanceolata, acuminata, 13–15 mm longa, 3–4 mm lata, roseo-rubra. Petala coccinea, lanceolata, acuta vel subacuminata, 9–10 mm longa, ca. 3 mm lata. Filamenta antise-pala 8–9 mm longa antipetala 6–7 mm longa, antheris oblongis, 2.5–3 mm longis ca. 2 mm latis. Stylus laxe villosus, stigmate capitato apice leviter 4-fisso, ca. 2 mm longo, 2–3 mm lato. Bacca matura non visa.

Densely pilose, many-branched shrub ca. 2 m tall. Branchlets subterete, 1.5–4 mm thick, pilose, with copper-colored bark. Leaves opposite to quaternate but usually appearing fasciculate due to the very reduced lateral shoots, firmly membranous, linear, acute at both ends; 20–70 mm long, 2–3 mm wide, subglossy dark green and sparsely strigose above, pale and densely pilose below along central nerve and margin; secondary veins mostly inconspicuous, midvein strongly prominent below, margin strongly revolute. Petioles 0.2–2 mm long. Stipules dark, lance-linear, ca. 1.5 mm long, subpersistent. Flowers few and axillary near the branch tips. Pedicels 16–18 mm long. Ovary oblong, 4–5 mm and ca. 2 mm thick. Floral tube narrowly funnelform, 33–37 mm long, 2.5–3 mm wide and bulbous at the base, narrowed to ca. 2 mm wide above the nectary and gradually widened above until 5–6 mm wide at the rim, loosely strigose-pilose outside, pilose inside in lower ½. Sepals lanceolate, acuminate, 13–15 mm long, 3–4 mm wide. Tube and sepals rose red. Petals scarlet, lanceolate, acute to subacuminate at the apex, 9–10 mm long, ca. 3 mm wide. Nectary unlobed, ca. 1.5 mm high. Filaments red, 8–9 mm and 6–7 mm long; anthers oblong, 2.5–3 mm long and ca. 2 mm wide, cream yellow. Style red, loosely villous for most of its length; stigma capitate, slightly 4-lobed at the apex, 2 mm long, 2–3 mm wide, exserted 1–3 mm beyond the anthers. Berry not seen.

Distribution: Known only from the type locality on the eastern slopes of the Andes in southernmost Ecuador (Fig. 56).

This is an unmistakable species because of its linear, revolute leaves and dense, pilose pubescence. It comes from a very poorly known area of Ecuador that is still accessible only by foot or by mule. Further collections would be desirable to determine the extent of variability in leaf shape and the probable affinities of this species. It is named in honor of Dr. Julian Steyermark, undoubtedly the foremost neotropical plant collector of this century.

8. ***Fuchsia nigricans*** Linden ex Planchon, Fl. Serres Jard. Eur. 5: *t.* 481. 1849. TYPE: Venezuela, Edo. Mérida, between Mendoza and Timotes, entrance to Paramillo de la Mucutí, 2,270–2,600 m, 1843, *Jean Jules Linden* 368 (P, holotype; BM, G 2 sheets, K, LE, TCD 2 sheets, US, W 2 sheets, isotypes). This same collection number at OXF was used as the type for *F. caracasensis* Fielding & Gardner, Sert. Pl. *t.* 29. 1844; that specimen is different from those listed above, however, and is a natural hybrid of *F. nigricans* and *F. gehrigeri* (see discussion on p. 43). Most of these collections have printed localities on the labels such as “Caracas” or “entre Caracas et Mérida,” but the actual locality is given by Linden in the protologue. Fig. 21.

Fuchsia atrorubra I. M. Johnston, Contr. Gray Herb. 75:31. 1925. TYPE: Colombia, Dept. Risaralda (formerly Caldas), Santa Elena, above Santuario, 2,000–2,300 m, 7–13 Sept. 1922, *Francis W. Pennell* 10313 (GH, holotype; NY, isotype).

Fuchsia sylvatica sensu Munz, Proc. Calif. Acad. Sci. IV. 25:68, pl. 11, fig. 58. 1943, pro parte.

Fuchsia adpressipilis Steyermark, Fieldiana Bot. 28:438. 1952. TYPE: Venezuela, Edo. Lara, between Santo Domingo and Los Quebraditos, S of Las Sabanetas, above Humocaro Bajo, 2,439–2,475 m, 8 Feb. 1944, *Julian A. Steyermark* 55381 (F, holotype; NY, isotype).

Erect to scandent shrubs 1–3 m tall with suberect to spreading branches. Young growth densely canescent with appressed or less often suberect hairs; branchlets terete, 2–5 mm thick, dull purple to light green; older branches with light brown, splitting bark. Leaves mostly ternate, opposite or rarely quaternate, membranous, smooth to sulcate nerved, mostly elliptic or obovate, but also spatulate or subpanduriform, acute to attenuate or cuneate at the base and sometimes noticeably unequal, acute to rounded at the apex, (4–)7–15(–18) cm long, (2–)3–8(–9) cm wide, medium-dark green and strigillose to subglabrous above, pale green and strigillose below, especially along the veins; secondary veins 11–16(–20) on either side of the midvein, sometimes red tinged; margin remotely gland-denticulate. Petioles strigillose, 12–35(–48) mm long. Stipules narrowly triangular, dark purple, 1–2 mm long, ca. 0.8 mm wide, succulent at the base, subulate at the apex, subpersistent. Flowers few to numerous, axillary in upper leaf nodes or in terminal bracteate racemes; rachis 4–22 cm long; bracts narrowly elliptic, short petiolate, loosely spaced. Pedicels slender, 3–9 mm long, suberect in bud to divergent or drooping at anthesis. Ovary narrowly cylindric-fusiform, densely canescent or strigillose, 6–11 mm long, 2–3 mm thick. Floral tube subcylindric, 14–22 mm long, 1.5–3 mm wide and slightly bulbous at the base, gradually widened above until 3–5(–6) mm wide at the rim, canescent-strigillose outside, densely pilose inside in lower $\frac{1}{2}$. Sepals lanceolate, acute, 6–10 mm long, 3–4 mm wide, spreading at anthesis. Tube and sepals pale pink to lavender or light red. Petals much darker, generally dark purple, narrowly elliptic-oblong, acute, 5–10 mm long, 2–3.5 mm wide, suberect to spreading at anthesis. Nectary green, shallowly 4-lobed, ca. 1.5 mm high. Filaments deep purple, 5–6 mm and 3–4 mm long; anthers oblong, 1.5–2 mm long, ca. 1 mm wide, dull white. Style glabrous, pink to purple; stigma capitate, subtetragonous, 2–3 mm long, 2–3.5 mm wide, 4-lobed in upper $\frac{1}{2}$, pink, slightly exserted beyond the anthers or in contact with the antesealous stamens at anthesis. Berry cylindric, 15–25 mm long, 6–10 mm thick, dull green to flushed purple, strigillose, slightly verrucose before maturity; seeds tan, 1.3–1.6 mm long, ca. 0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Venezuela and Colombia. Scattered to locally frequent shrubs in forest openings, streambanks, along roadsides, and in moist thickets in mid-elevation cloud forest; in Venezuela, from Lara to Táchira at 2,100–2,650 m; in Colombia, in all three cordilleras: in the Cordillera Oriental known only from Norte de Santander near the Venezuelan border; in the Cordillera Central in Tolima, Quindío, Caldas, and Antioquia; in the Cordillera Occidental from Antioquia south to Cauca; 1,700–2,700 m (Fig. 57).

Representative specimens examined: VENEZUELA, LARA: below La Sabaneta, 15 km from Los Naranjos above Humocaro Bajo, *Berry & Azuaje* 2500 (MERF, MO); trail from Humocaro to Buenos Aires, below Páramo de Las Rosas, *Liesner et al.* 8001 (MO), 8215 (MO, VEN). MÉRIDA: La Culata

to El Valle, *Badillo* 5587 (MY); between El Morro and Aricagua, Loma de la Vagabunda, *Badillo* 6567 (MY); Guaraque to Tovar, *Benitez de Rojas* 2076 (MY); La Mosquera, Mucuquí, above Pueblo Nuevo, *Bernardi* 232 (NY); Monte Zerpa, *Bernardi* 653 (NY); 10 km above La Azulita to La Carbonera, *Berry & Centeno* 2513 (MER, MERF, MO); 1 km below Chachopo on road to Timotes, *Berry* 3131 (MO, VEN); 4 km below San Eusebio to La Azulita, *Berry* 3454 (MO, VEN); La Carbonera, *Berry* 3451 (MO); between La Mucuy and Mesa de los Pinos, *Berry* 3438 (MO, VEN); Páramo de la Sal, *Jahn* 507 (VEN); above Palmira, *Jahn* 509 (US, VEN); Páramo de Aricagua, *Jahn* 1028 (US, VEN); road to El Morro, *Jahn in* 1910 (VEN); El Filo, between Guaraque and Tovar, *López-Palacios* 8 (MER); trail from La Escalera to Puente de La Escalera, *Luteyn et al.* 6208 (MO); road to Páramo de los Colorados, *Quintero et al.* 1280 (MER); El Chorotal, *Quintero* 1616 (MER); Tienditas del Chama to Aricagua, *Quintero & Ricardi* 1772 (MER); between El Chorrerón and La Cueva, road to Páramo de Palmira, Dpto. Miranda, *Ruiz-Terán & Dugarte* 12493 (MERF); Quebrada La Honda, E of Los Nevados, Dpto. Libertador, *Ruiz-Terán* 12090 (MO); between Los Corales and Los Cuadros, *Steyermark* 55769 (F, US); 2 km above Las Tapias, S of Bailadores, *Tillett & Hönig* 738-465 (MO, VEN); road from Manzano Alto to Páramo de los Conejos, ca. 7 km NE of Mérida, *Wessels-Boer* 2245 (MER, MO, U). TÁCHIRA: 13 km E of El Portachuelo, road to Pregonero, *Berry* 3288 (MO, VEN); 2 km E of Zumbador, road to Queniquea, *Berry* 3294 (MO, VEN); 15 km E of Zumbador to Queniquea, *Berry* 3304 (MO, VEN); between Zumbador and San Isidro, *Bunting* 2548 (GH, MY); Páramo el Pantano, *Charpin et al.* 13446 (G); Quebrada Agua Azul, S of El Reposo, *Steyermark & Liesner* 118431 (MO, VEN). TRUJILLO: Campo Elías to Boconó, *Badillo* 4965 (MY); 12 km W of San Rafael, old road Boconó-Trujillo, *Berry* 3103 (MO, VEN), 3104 (MO, VEN); 5 km above La Mesa de Esnujaque, road to Dury, *Berry* 3130 (MO); 8 km W of El Batatal to Boconó, *Berry* 3093 (MO, VEN); 3095 (MO, VEN); Agua Obispo, *Funck & Schlim* 797 (BM, CGE, F, G, LE, OXF, P 2 sheets, W); Río de Agua Negra, near Boconó, *Lasser* 1175 (US, VEN); Misisí, slopes of Páramo de la Cristalina, *Ruiz-Terán & López-Palacios* 7635 (MERF, MO); Páramo de Guaramacal, 15 km from Boconó, *Ruiz-Terán* 9224 (MERF, MO). COLOMBIA, ANTIOQUIA: Santa Elena, *Archer* 1195 (US 2 sheets); near Nariño, *Barkley & Johnson* 180826 (COL, RSA, US). CALDAS: Mt. Cardal, *Tracey* 344 (K). CHOCÓ: N of Albán, *Dugand & Jaramillo* 3040 (COL, US); Quebrada El Sucio above Carmen de Atrato, *Fosberg & Core* 21550 (RSA, S, US). NORTE DE SANTANDER: Ocaña to Pamplona, *Kalbreyer/Sisale* 1104 (K); Prov. of Ocaña, *Schlim* 338 (P). QUINDÍO: Río Santa Rita, Salento, *Killip & Hazen* 8966 (GH, NY, PH, US); Río Quindío, Salento, *Pennell* 10099 (GH); Salento, *Pennell & Hazen* 10144 (GH, NY, PH, US). TOLIMA: Alto San Juan-Quindío, *André* 2072 (K); Quindío, *André s.n.* (K); La Suiza, above Ibagué, *Cuatrecasas* 3260 (MA); Las Juntas, Combayeque, *Goudot* 3 (P); Río Toche to Machín, *Killip & Hazen* 9564 (GH); Río Combeina, Juntas, *Schneider* 1156 (COL, S); Toche, *von Sneidern* 3090 (COL, S); la Mediación, Quindío, *Triana* 3811 (G, K, W). VALLE: above Las Brisas, between El Tabor and Alto de Mira, *Cuatrecasas* 22425 (F, RSA, VALLE).

This species is vicarious with *Fuchsia sylvatica*, which differs in a series of minor characters such as lighter colored petals, narrower fruits, more rugulose leaves, and denser, more cordate bracts. They are geographically separated by the Río Patía valley in the Cordillera Occidental of southern Colombia. The pattern of distribution of these two species suggests a northern origin in the Cordillera Oriental of Colombia and Venezuela, where *F. nigricans* is now most common and widespread. As with at least three other species in the section, it may have spread westwards into the Cordillera Central and Cordillera Occidental; *F. nigricans* is not found south of 3°N Latitude or in the Nudo de Pasto area. *Fuchsia sylvatica* may have diverged secondarily south of the Patía barrier, where it is now restricted on the western slopes of the Cordillera Occidental in Ecuador. If a northwards migration route had been used, one would expect to find members of these species in the Nudo de Pasto or in the southern parts of the Colombian cordilleras, but this is not the case.

Fuchsia nigricans and *F. sylvatica* are distinguished from their congeners by their fine, ashy pubescence; the short-pedicellate, elongate ovaries and fruits; the petals darker than the tube or sepals; and the subtetragonous stigma. The closest relative is *F. pallescens*, which occurs on the opposite side of the Ecuadorian Andes from *F. sylvatica* and which shares the subracemose flowers, darker pet-

als, and elongate ovaries on short pedicels. It differs, however, in its pale whitish floral tube, semisucculent stems, and thin membranous, long petiolate leaves. *Fuchsia sessilifolia* also has small bicolored flowers with short pedicellate, elongate fruits, but the flowers are borne in panicles, and the leaves are sessile, lanceolate, and quaternate.

Fuchsia nigricans is the most widespread of the Venezuelan fuchsias and occurs continuously from Lara to Táchira. It is surprisingly absent from most of the Colombian side of the Cordillera Oriental, however. In Colombia, it is only one of two species that occurs in all three cordilleras. With this wide range it is found sympatrically with five species, *F. gehrigeri*, *F. putumayensis*, *F. sessilifolia*, *F. venusta*, and *F. verrucosa*. Hybrids have been found with all of these except *F. verrucosa*; a detailed analysis of the different hybrids is included in the section on interspecific hybridization.

9. ***Fuchsia sylvatica*** Benth. Pl. Hartw. 176. 1845. Munz, Proc. Calif. Acad. Sci. IV. 25:68. 1943, pro parte; Opera Bot., Ser. B, 3:23. 1974, pro parte. TYPE: Ecuador, Prov. Pichincha, woods at Guayán, W slopes of Volcán Pichincha, 1841–1843, *Theodor Hartweg* 984 (K Benth. Herb., holotype; photograph, MO; BM, BREM, CGE 2 sheets, G, K Hooker Herb., LE, OXF, isotypes).

Erect to scandent shrubs 1–2.5 m tall. Young growth finely canescent; older stems with tan, fissured bark. Leaves mostly ternate, opposite, or rarely quaternate, membranous, finely reticulate-veined and sometimes rugulose, elliptic to (ob-)ovate, acute to attenuate at the base, mostly acute at the apex, 4–15 cm long, 2–8 cm wide, medium-dark green and strigillose above, pale green to tinged red and strigillose below; secondary veins 11–18 on either side of the midvein; margin remotely gland-denticulate. Petioles strigillose, 6–34 mm long. Stipules dark purple, narrowly triangular, 1–2 mm long, ca. 0.7 mm wide, thick at the base, subulate at the apex, subpersistent. Flowers generally numerous in long, straggly, terminal or subterminal racemes; rachis arching-pendant or sometimes $\pm$ twisted, 5–20 cm long; bracts ovate-cordate, sessile, tightly grouped. Pedicels slender, divergent to pendant, 3–10 mm long. Ovary narrowly cylindric-fusiform, often narrowed towards the apex, 6–10 mm long, 2–3 mm thick. Floral tube narrowly funnelform, 14–22 mm long, 2–3 mm wide and slightly bulbous at the base, gradually widened above until 3.5–7 mm wide at the rim, canescent-strigillose outside, pilose inside in lower $\frac{1}{2}$. Sepals lanceolate, acute, 10–13 mm long, 3–5 mm wide, spreading at anthesis. Tube and sepals red to rose red. Petals darker, crimson, narrowly elliptic-oblong, acute, 5–10 mm long, 2–4 mm wide. Nectary green, shallowly 4-lobed, ca. 1.5 mm high. Filaments red, 5–7 mm and 3–5 mm long; anthers oblong, 1.5–2 mm long, ca. 1 mm thick, dull white. Style glabrous to sparsely pilose, light red; stigma capitate, subtrigonous, 2–3 mm long, 2–4 mm wide, 4-lobed in upper $\frac{1}{2}$, pink, slightly exserted beyond the anthers. Berry subcylindric-fusiform, gradually narrowed towards the apex, $\pm$ verrucose before maturity, 13–17 mm long, 5–7 mm thick, red purple to subtranslucent; seeds ca. 1.5 mm long, ca. 0.8 mm wide. Gametic chromosome number $n = 11$.

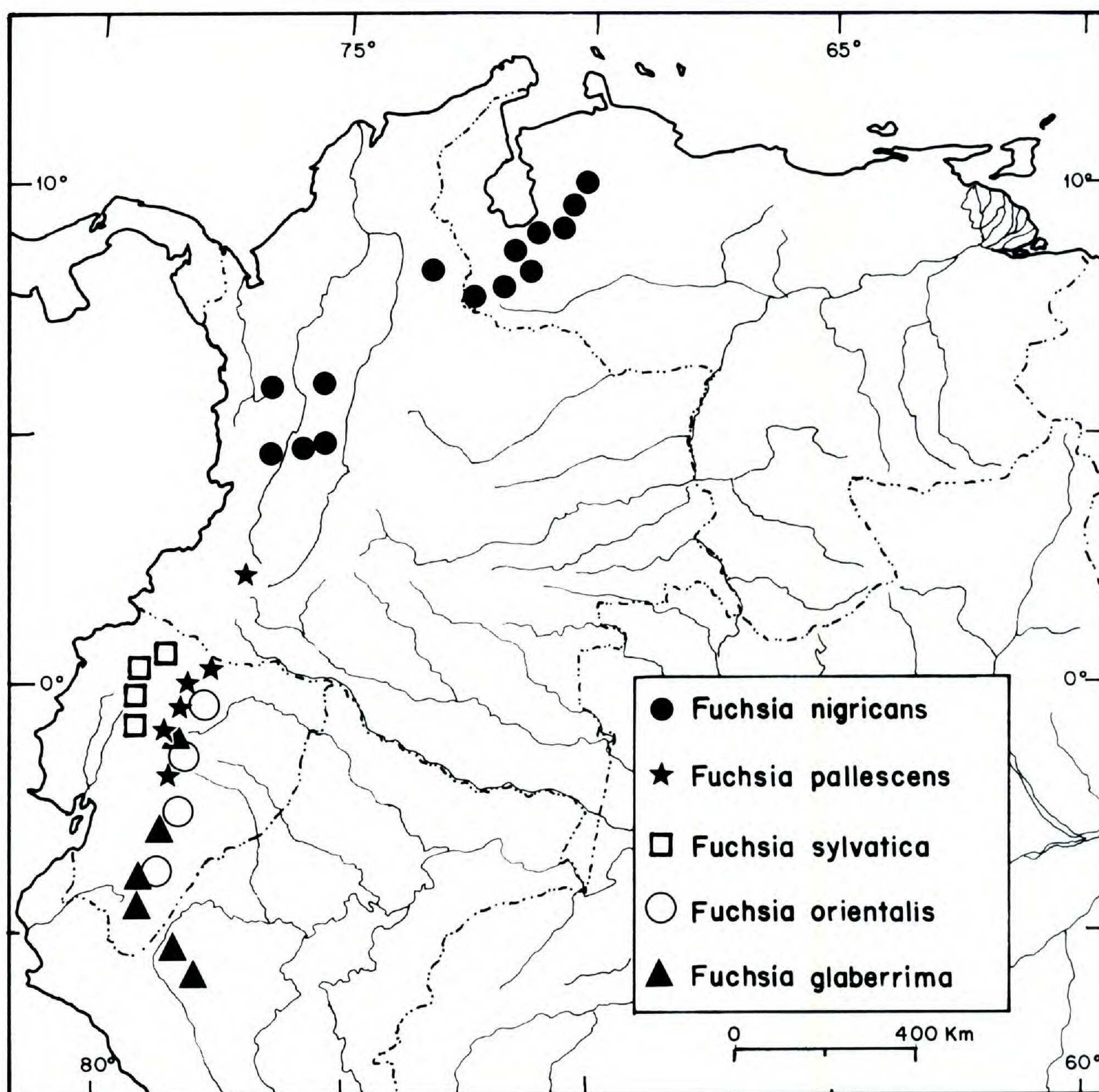


FIGURE 57. Distribution of the *Fuchsia nigricans* species group.

Distribution: Ecuador. Scattered shrubs on the western slopes of the Andes from Cotopaxi to Imbabura Provinces, in mid-elevation cloud forest, growing in moist soil in thickets, along streams, or on roadside banks; 2,600–3,100 m (Fig. 57).

Representative specimens examined: ECUADOR, COTOPAXI: 5 km above Pilaló towards Latacunga, *Berry & Berry* 2550 (MO); 4 km E of Pilaló, *Escobar* 1095 (MO). IMBABURA: 25 km W of Laguna Cuicocha on road to Intá, *Berry* 3171 (MO, QCA). PICHINCHA: Los Alpes, NW side of El Corazón, *Acosta Solis* 7074 (F); 26 km from Chillogallo towards Chiriboga, *Berry* 2537 (MO, Q); Km 32–33 W of Chillogallo, *Berry & Escobar* 3237 (MO), 3238 (MO), 3239 (MO), 3240 (MO); Siglal, above Chiriboga, *Berry & Escobar* 3244 (MO); 11–12 km NW of Nono, *Croat* 38823 (MO); W side of Volcán Pichincha, *Jameson* 709 (BM, G, K, LE, OXF 2 sheets); valley of Lloa, *Jameson* s.n. (K); Km 32–38 old road Quito to Santo Domingo de los Colorados, *Luteyn & Lebrón-Luteyn* 5608 (MO, NY); Alaspongo, trail from Nono to Guala, *Mexia* 7703 (BM, GH, K, MO, NY, POM, S, U, UC, US).

This species is closely related to *F. nigricans*, and their differences, distributions, and relationships are discussed under that species. It occurs sympatri-

cally with *F. macrostigma*, *F. scabriuscula*, and *F. sessilifolia*. No flowering hybrids were found with any of these species, but it is likely that nonflowering hybrids were growing between Nono and Nanegal, where I found a dense thicket of *F. scabriuscula*, *F. sessilifolia*, and *F. sylvatica* growing together in direct contact in 1977. The vegetative similarity of *F. scabriuscula* and *F. sylvatica* makes confirmation of this problematical, however.

On the western slopes of Prov. Carchi along the Colombian border, plants were found that agreed well with *F. sylvatica* in all morphological characters except for their much longer flowers and fruits. Floral tubes are 45–54 mm long and fruits ca. 23 mm long in *Holm-Nielsen et al.* 5752 (AAU, S; Ecuador, Prov. Carchi, Km 60 of Tulcán-Maldonado road, 2,700 m) and *Berry* 3149 (MO, QCA; 68 km W of Tulcán to Maldonado, 2,500 m). Pollen stainability in these collections is high, 88.8% in *Holm-Nielsen et al.* 5752 and 94.2% in *Berry* 3149 (500 grains counted). More intensive collections are needed from this and surrounding areas, because it is very rich in intermediate forms and local endemics (see *F. cinerea*, *F. corollata*, *F. dependens*, and *F. polyantha*).

10. ***Fuchsia pallescens*** Diels, Notizbl. Bot. Gart. Berlin-Dahlem 14:34. 1938. Munz, Proc. Calif. Acad. Sci. IV. 25:29. 1943; Opera Bot., Ser. B, 3:20. 1974. TYPE: Ecuador, Prov. Tungurahua, E of Patate, woods above Leito, 2,750 m, 8 March 1935, *Arnold Schultze-Rhonhof* 1827 (B, holotype, destroyed in World War II). NEOTYPE: Ecuador, Prov. Tungurahua, vicinity of Patate, Hacienda Leito, 2,800 m, 5 Aug. 1939, *Erik Asplund* 8073 (S; photograph MO).

Usually well-branched herbs to subshrubs 5–18 dm tall. Branchlets subterete, semisucculent, 2–4 mm thick, subglabrous; older stems 4–8 mm thick, with dull tan, finely fissured bark. Leaves opposite or ternate, thin membranous, elliptic-ovate, attenuate to rounded at the base, subacuminate at the apex, 3.5–7(–9.5) cm long, 1.5–4(–5) cm wide, velvety dark green and glabrous to strigillose above, paler below and subglabrous to puberulent, especially along the veins; secondary veins 5–7(–9) on either side of the midvein, lightly impressed above and subelevated below; margin gland-denticulate. Petioles slender, (15–)25–40(–50) mm long, glabrous to puberulent, green. Stipules triangular, 1–1.5 mm long, ca. 0.5 mm wide, succulent at the base, sometimes connate and reflexed on lower nodes, subpersistent. Flowers few and pendant in upper leaf axils or subracemose at the tips of branches with reduced leaves 10–20 mm long subtending the flowers. Pedicels slender, drooping, 7–15 mm long. Ovary narrowly cylindric, 5–8 mm long, 2–3 mm thick. Floral tube narrowly funnelform, 18–25 mm long, slightly nodose at the base and 1.5–2 mm wide, gradually widened above until 4–5 mm wide at the rim, glabrous to puberulent outside, densely pilose inside in lower ½. Sepals lanceolate, acute to long acuminate, 9–15 mm long, 3–4 mm wide, spreading at anthesis. Tube and sepals subnitid whitish pink to pale red. Petals considerably darker, maroon to dark red, broadly elliptic, acute to rounded at the apex, 5–8 mm long, ca. 4 mm wide, suberect. Nectary unlobed, 1–1.5 mm high. Filaments light pink, 5–7 mm and 3–5 mm long; anthers oblong, 1–1.5 mm long, ca. 0.8 mm wide, cream to pale yellow. Style glabrous, light pink; stigma capitate, 4-lobed in upper ½, 1.5–2.5 mm long, 2–3 mm wide, white. Berry oblong,

narrowed apically, rugose before maturity, turning lustrous purple, ca. 13 mm long, 4–6 mm thick; seeds ca. 1 mm long, 0.6–0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuador and southern Colombia. Moist, shady cloud forest habitats, restricted to the eastern slopes of the Andes in Ecuador from Azuay to Napo, and disjunct to the west slopes of the Cordillera Occidental in Cauca, Colombia; 2,550–2,900 m (Fig. 57).

Specimens examined: COLOMBIA, CAUCA: near ridge of Cordillera Occidental, Km 41 of Popayán-UrIBE-Munchique road, *Berry* 3570 (COL, MO); Mount El Derrumbo, *Killip* 7992 (NY, PH, US), *Lehmann* 5956 (K). ECUADOR, CHIMBORAZO: road from Pusucucho to El Placer, *Acosta Solis* 7255 (F), 7281 (F). IMBABURA: Trail to Río San Pedro, ridge S of Río Clavadero, E of Cayambe, *Wiggins* 10444 (DS, NY, POM). NAPO: Km 209 of Quito-Baeza road, below Papallacta, *Berry & Berry* 2524 (MO, Q), 2527 (MO, Q); above Cuyuja, *Berry & Escobar* 3248 (MO); Salcedo (San Miguel), Km 55 on Salcedo-Napo road, *Boeke* 901 (MO); Santa Bárbara de Sucumbios, 10 km E of Santa Bárbara, *Harling* 4105 (S); between Cuyuja and Papallacta, *Holm-Nielsen et al.* 6815 (AAU, NY, S). TUNGURAHUA: between Leito and La Cima, *Acosta Solis* 9025 (F); between La Cima and Río Chico, *Acosta Solis* 10242 (F). AZUAY: Quebradas leading into the Río Collay, 3–8 km N of Sevilla de Oro, *Camp* 4897 (GH, NY, RSA, US).

This species is allied to *F. nigricans* and *F. sylvatica* in its subracemose inflorescence of short flowers with dark petals and elongate ovaries. The tube and sepals are unusually pale, however, and the plants are generally more delicate, with thin leaves and semisucculent young stems. Small, nearly herbaceous plants of *F. pallescens* are commonly found growing under large *Gunnera* leaves, though larger, woodier plants can sometimes be found in more open areas such as roadbanks. It occurs sympatrically with *F. scabriuscula* and *F. vulcanica*.

Fuchsia pallescens occupies ranges distinct from both *F. nigricans* and *F. sylvatica*. The disjunction from western Colombia to the eastern slopes of Ecuador is similar to that of *F. putumayensis* and is possibly due to a past migration across the Nudo de Pasto.

The limited number of specimens available makes an accurate assessment of the variability of this species difficult, but three variants can be mentioned: 1) *Harling* 4105 (S), from northern Napo near the Colombian border. The petioles of this collection are short, and the leaves have 8 or 9 secondary veins instead of the normal 5 or 6. Pollen stainability of this individual is 60% (500 grains). 2) *Camp* 4897 (GH, NY, RSA, US), from Azuay. The floral tubes of this collection are short (ca. 18 mm), as are the nonacuminate sepals, and the petals may not be as dark as in other populations. 3) Colombian collections. *Berry* 3570 is puberulent and has a few more leaf veins, but otherwise is similar to the main Ecuadorian populations. *Killip* 7792 (NY, PH, US) and *Lehmann* 5956 (K) have rather stout stems and larger leaves. The tube and sepal color cannot be determined from these specimens, however, so their placement in this species should be considered tentative.

11. ***Fuchsia orientalis*** P. Berry, sp. nov. TYPE: Ecuador, Prov. Napo, between Cosanga and Baeza, trailside in open woods, 2,000 m, 5 May 1935, *Ynes Mexia* 7337 (US 1662406, holotype; photograph, MO; K, NA, UC, isotypes).

Fuchsia sylvatica sensu Munz, Opera Bot., Ser. B, 3:23. 1974.

Frutex 1–2 m altus, ramulis foliis junioribus puberulo-strigulosus. Folia opposita, raro ternata, membranacea, anguste elliptica vel obovata, basi acuta, attenuata vel inaequalia, apice acuta vel acuminata, 6–21 cm longa, 2.5–6 cm lata, supra subnitida subglabrataque subtus pallidioria nervis marginibusque plerumque strigulosus vel puberulis; nervis secundaris utroque latere 12–17 subtus plerumque prominentibus, margine integerrima; petiolis strigulosus, 8–20 mm longis; stipulis lanceolatis, subpersistentibus, 1.5–3 mm longis, 0.5–0.8 mm latis, in nodis veteribus crassiusculis et recurvatis. Flores scarlatini vel aurantiaco-rubri, pauci vel numerosi in racemis abruptis terminalibus vel axillaribus dispositi; rhachidi 5–16 cm longa; bracteis persistentibus lanceolatis 10–25 mm longis, 3–10 mm latis, petiolis 3–5 mm longis; pedicellis 3–7(–12) mm longis; ovario oblongo, 4–5 mm longo. Tubi florales anguste infundibuliformes 15–21 mm longi, basi ca. 2 mm lati et parum bulbosi inde leviter constricti superne gradatim dilatati summo 3.5–5 mm lati, extus strigulosi intus infra medium retrorso-villosi. Sepala oblongo-lanceolata, 6–8 mm longa, 3–4 mm lata. Petala late elliptica, 5–8 mm longa, 3–4 mm lata. Filamenta antiseipala 6–7 mm longa, antipetala 4–5 mm longa, antheris late oblongis, ca. 1.5 mm longis, ca. 1 mm latis, albidis. Stylus ruber plerumque glaber, stigmate capitato 1.5–2 mm longo, ca. 2.5 mm lato apice leviter 4-fisso. Bacca cylindrica, verrucosa, 9–12 mm longa, ca. 5 mm crassa, rubro-purpurea; seminibus 1–1.1 mm longis, ca. 0.7 mm latis. Numerus gameticus chromosomatum $n = 11$.

Shrubs 1–2 m tall. Young growth puberulent to strigillose. Leaves opposite, rarely ternate, membranous, narrowly elliptic to obovate, acute to attenuate or unequal at the base, acute to acuminate at the apex, 6–21 cm long, 2.5–6 cm wide, subnitid and subglabrous to strigillose above, paler and mostly strigillose or puberulent along the veins and margin below; secondary veins 12–17 on either side, mostly prominent below, margin entire. Petioles strigillose, 8–20 mm long. Stipules lanceolate, 1.5–3 mm long, 0.5–0.8 mm wide, mostly persistent and becoming thick and recurved on lower nodes. Flowers few to many in abrupt, terminal and axillary, bracteate racemes; rachis 5–16 cm long, elongating in fruit; bracts lanceolate, persistent, 10–25 mm long, 3–10 mm wide, with petioles 3–5 mm long. Pedicels strigose, 3–7(–12) mm long. Ovary cylindrical, 4–5 mm long, 1.5–2 mm thick. Floral tube narrowly funnelform, 15–21 mm long, ca. 2 mm wide and slightly bulbous at the base, gradually widened above until 3.5–5 mm wide at the rim, strigillose outside, retrorse villous in lower $\frac{1}{2}$. Sepals oblong-lanceolate, 6–8 mm long, 3–4 mm wide. Tube and sepals scarlet to orange red. Petals red to orange red, oblong to broadly elliptic, 5–8 mm long, 3–4 mm wide. Nectary unlobed or shallowly lobed, 1–1.5 mm high. Filaments red, 6–7 mm and 4–5 mm long; anthers broadly oblong, ca. 1.5 mm long and ca. 1 mm wide, white. Style red, mostly glabrous; stigma capitate, 1.5–2 mm long, ca. 2.5 mm wide, 4-cleft at the apex. Berry cylindrical, verrucose, 9–12 mm long, ca. 5 mm thick, red purple; seeds 1–1.1 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuador. Scattered shrubs in low elevation cloud forest on the eastern slopes of the Andes from Napo to Zamora-Chinchipe, 1,200–2,600 m (Fig. 57).

Specimens examined: ECUADOR, AZUAY: 1–8 km N of Sevilla de Oro, *Camp E-4251* (NY, P, RSA). LOJA: 14 km E of Loja towards Zamora, *Berry & Escobar 3199* (MO, QCA); Km 10.5 of Loja-Zamora road, *Holm-Nielsen et al. 3552* (AAU, S). MORONA-SANTIAGO: between Río Soldo and La Esperanza, road to Huamboya, *Acosta Solis 7343* (F); Cordillera de Cutucú, W slopes, between Logroño and Yaupi, *Madison et al. 3342* (MO); trail between Mirador and Pailas, *Steyermark 54280* (NY). NAPO: Cordillera Guacamayo, slope toward Urcusiqui, *Asplund 9578* (S); Cosanga, 20 km S of Baeza, *Balslev & Madsen 10340* (AAU, MO); 10 km from Baeza to Cosanga, *Berry & Escobar 3246* (MO); Cerro Antisana, E of Borja, *Grubb et al. 1050* (K, NY); Río Cosanga, near Cosanga, *Kirkbride & Chamba*

4012 (MO). TUNGURAHUA: Río Mapoto, *Penland & Summers* 282 (F, GH, POM, RSA). ZAMORA-CHINCHIPE: Huaico, SE of Loja, *Espinosa E-660* (RSA); Km 16 Loja to Zamora, *Sparre* 16507 (S).

This species typically has elongate racemes with persistent, narrowly lanceolate bracts. This character is also found in the larger leaved *F. pilosa*, but *F. orientalis* is most closely allied to *F. glaberrima*, which has larger flowers and more sessile leaves, but similar thick stipules and persistent bracts. In Napo, it is a low elevation species on slopes leading down into the "Oriente" or Amazon lowlands of Ecuador. It occurs sympatrically there with *E. scabriuscula*. In southern Ecuador, it occurs between 2,000 and 2,600 m, considerably higher than in the north.

12. *Fuchsia glaberrima* I. M. Johnston, *Contr. Gray Herb.* 75:32. 1925. Macbr., *Field Mus. Nat. Hist., Bot. Ser.* 13(4):555. 1941. Munz, *Proc. Calif. Acad. Sci.* IV. 25:66, *pl. 10, fig. 55*. 1943; *Opera Bot., Ser. B*, 3:15. 1974. TYPE: Ecuador, Prov. Tungurahua, valley of Río Pastaza, between Baños and Cashurco, 1,300–1,800 m, 25 Sept. 1923, *Albert S. Hitchcock* 21750 (GH, holotype; photograph, MO; NY, US, isotypes; photograph of US isotype, UC).

Simple to few-branched shrubs 1–3 m tall. Branchlets subterete, 3–5 mm thick, glabrous or minutely and sparsely puberulent on youngest growth, green to red-purple. Leaves opposite or subopposite near the branch tips, firmly membranous to subcoriaceous, oblanceolate, obtuse to attenuate at the base, acute to acuminate at the apex, 10–24 cm long, 4–8 cm wide, subnitid and glabrous above, pale to usually flushed red-violet below and glabrous to finely puberulent along the nerves; secondary veins 8–20(–26) on either side of the midvein; margin entire. Petioles short, stout, 3–8 mm long. Stipules triangular, thick, mostly connate and recurved between the lower, opposite leaves, 2–3 mm long, 2–4 mm wide, persistent. Flowers 3–ca. 15 in terminal, bracteate, drooping racemes; rachis 2–4 cm long or occasionally extending 6–12 cm long in fruit; bracts sessile, lanceolate, 10–30 mm long, subtending the alternately disposed flowers. Pedicels 3–12 mm long, mostly glabrous. Ovary oblong, 7–9 mm long, 2–3 mm thick. Floral tube narrowly funnelform, 22–35(–40) mm long, ca. 2 mm wide at the base, slightly constricted above the nectary, then gradually widened above until 6–7 mm wide at the rim, glabrous outside, densely pubescent inside for most of length. Sepals oblong-lanceolate, 8–11 mm long, 4–5 mm wide, shortly acute-tipped, subtetragonous in bud, spreading at anthesis. Tube and sepals red to orange red. Petals red, broadly elliptic-obovate, 7–11 mm long, 5–6 mm wide, rounded at the apex. Nectary unlobed, ca. 1.5 mm high. Filaments red, 5–6 mm and 3–4 mm long; anthers oblong, ca. 2 mm long, ca. 1 mm wide. Style densely pilose or occasionally glabrous; stigma capitate, subtetragonous, ca. 2 mm long, ca. 3 mm wide, 4-lobed apically, shortly exserted beyond the anthers. Berry oblong, ca. 15 mm long, 7–9 mm thick; seeds ca. 2 mm long, ca. 1 mm wide.

Distribution: Scarce shrubs of the lower cloud forest limit from Tungurahua, Ecuador, to Amazonas, Peru, 1,600–1,900 m (Fig. 57).

Specimens examined: ECUADOR, LOJA: W slopes of Cordillera del Cóndor NW of Nudo de Sabanilla, around Tambo Cachiyacu, SE of Yangana, *Steyermarck* 54786 (NY). MORONA-SANTIAGO: Plan de Milagro, ca. 10 km NW of Indanza, *Jorgensen OHJ-38* (NY); W slopes Cordillera de Cutucú, trail

from Logroño to Yaupi, *Madison et al.* 3531 (MO). TUNGURAHUA: upper Río Pastaza, *Spruce* 5031 (K). ZAMORA-CHINCHIPE: Río de San Francisco, *Poortman* 318 (P). WITHOUT LOCALITY: *Lobb s.n.* (K); *Pearce* 329 (K). PERU, AMAZONAS: 12–20 km E of La Peca, Serranía de Bagua, *Barbour* 2581 (MO), 2668 (MO), 2686 (MO), 2718 (MO), 2734 (MO), 4171 (MO); *Gentry et al.* 23031 (MO), 23023 (MO); Yambrasbamba, *Mathews* 803 (OXF); Taulia, *Mathews* 1484 (K).

This species can be readily distinguished by its large, opposite, oblanceolate, and subsessile leaves that are usually violet flushed below. It also has unusually thick, persistent stipules. *Fuchsia glaberrima* closely resembles *F. orientalis* in its abrupt racemes, short pedicels, and persistent bracts, but the latter has shorter flowers and longer petiolate leaves. Both are restricted to the low, eastern slopes of the equatorial Andes, but they are not known to occur together or to intergrade.

This is the only species in the section to occur both north and south of the Amotape-Huancabamba zone in southern Ecuador and northern Peru. Plants from the southern end of the range (Amazonas and Loja) have more secondary veins (ca. 20 vs. ca. 10) and less hairy styles than central Ecuadorian collections. Their floral tubes are also somewhat longer (35 mm vs. 25 mm), and the inflorescences are looser and less congested. Both vein number and style pubescence can vary locally, however; *Gentry et al.* 23031 (MO) from Amazonas has fewer than 20 veins and a pilose style, but the close-by *Gentry et al.* 23023 (MO) has over 25 secondary veins and a glabrous style.

13. ***Fuchsia macrophylla*** I. M. Johnston, Contr. Gray Herb. 75:35. 1925. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):557. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:66, pl. 10, fig. 56. 1943. TYPE: Peru, Dept. Junín, La Merced, Hacienda Schunke, 1,200 m, Aug.–Sept. 1923, *Francis Macbride* 5616 (F 536655, holotype; photographs, NY, POM, UC; GH, US, isotypes).

Erect to scandent shrubs 1–3 m tall with spreading branches. Young growth minutely puberulent, branchlets 3–6 mm thick, usually red-purple tinged; older branches with light brown, finely fissured bark. Leaves opposite or less often ternate, firmly membranous, (narrowly) elliptic to lanceolate or (ob-)ovate, acute to cuneate at the base, acute to acuminate at the apex, basal leaves generally considerably larger than the upper ones, 16–27 cm long, 5–9 cm wide, light to dark green and subglabrous above, paler and subglabrous below; secondary veins 14–19 on either side of the midvein, reddish and prominent below, anastomosing into a distinct submarginal vein; margin subentire. Petioles subglabrous, 10–35 mm long, reddish. Stipules dark, lanceolate to triangular, sometimes connate, 1–2 mm long, 0.5–0.8 mm wide, mostly deciduous. Flowers few to numerous in short lateral racemes or on short side branchlets; rachis 2–10(–12) cm long. Pedicels slender, spreading, 10–26(–32) mm long, reddish. Ovary ellipsoid, 4–5 mm long, ca. 2 mm thick. Floral tube narrowly funnelform, 19–25 mm long, ca. 2 mm wide and slightly nodose at the base, gradually widened above until 4–6 mm wide at the rim, puberulent to subglabrous outside, pilose inside for most of length. Sepals lance-oblong, acute, 8–9 mm long, 3–4 mm wide, short-pointed in bud. Tube red, sepals red with green tips. Petals scarlet, elliptic to lanceolate, acute, 7–10 mm long, 3–4 mm wide. Nectary unlobed, ca. 1 mm high. Filaments red, 4–7 mm and 3–4 mm long; anthers oblong, 1.4–1.6 mm long, ca. 0.8 mm wide, dull white. Style pubescent for most of length, red; stigma capitate, ca. 2 mm long and wide,

shallowly 4-lobed, cream to pink, exserted 1–2 mm beyond anthers. Berry subglobose to ellipsoid, 10–13 mm long, 8–9 mm thick, nitid dark purple; seed tan, 1.1–1.3 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Central to southern Peru, from Loreto and Huánuco to Puno; in moist thickets in low elevation cloud forest and subtropical wet forest; 1,200–2,000 m (Fig. 56).

Representative specimens examined: PERU, AYACUCHO: 8 km below Jano, road from Tambo to Ayna, *Berry* 3053 (MO, USM); between Tambo San Miguel, Ayna, and Hacienda Luisiana, *Dudley* 11816 (F, MO, NA 2 sheets, NY, USM); Ccarrapa, between Huanta and Río Apurímac, *Killip & Smith* 22353 (F, GH, K, NY, S, US). CUZCO: Tunquimayo, Quince Mil, Prov. Quispicanchis, *Vargas* 11776 (CUZ, MO); between Tambomayo and Consuelo, along Río Tambomayo, Prov. Paucartambo, *West* 7113 (GH, MO, UC). HUÁNUCO: trail from Puente Durand to Éxito, Pampa Hermosa, *Mexia* 8142 (BH, BM, F, G, GH, K, MO, NA, NY, S, U, UC); cuesta San Toribio, quebrada Cutama, *Vargas* 5370 (BH, CUZ); Palo Marcado, *Vargas* 15336 (MO, USM). JUNÍN: 44 km W of Satipo towards Concepción, *Berry & Aronson* 3080 (MO, USM); Cumbre Yacunay above La Merced, *Hutchison* 1173 (F, G, GH, MICH, MO, NY, S, UC, US); Pichis trail, *Killip & Smith* 25436 (F, GH, NY, US); Pangoa, *Mathews* 1169 (K, OXF); Utcuyacu, *Woytkowski* 35382 (F, MO 2 sheets, UC, USM). LORETO: La Divisoria, *Ferreira* 1654 (MO, RSA, US 2 sheets, USM); below La Divisoria, *Ferreira* 4299 (MO, US, USM); vicinity of Aguaytía, *Mathias & Taylor* 5150 (F, RSA, US, USM). PASCO: San Luis de Oxapampa, *Infantes* 1492 (MO, USM); Vitoc, *Isern* 2556 (F); road to Pozuzo, *Pearce* 213 (K); Pozuzo, *Pearce* 541 (K); between La Merced and Oxapampa, *Saunders* 547 (BM); Quillasú, *Soukup* 3343 (COL); Villa Rica, *Woytkowski* 7325 (GH, MO). PUNO: trail between La Oroya and Mina Santo Domingo, *Hodge* 6025 (CUZ, GH, US, USM).

This species is closely allied to the only other two species in the section with lateral inflorescences, *F. ovalis* and *F. macropetala*. These inflorescences emerge from leaf axils in the mid-section of the stem and not apically as in most other species (Fig. 40). *Fuchsia ovalis* differs in its heavily pilose pubescence and long petiolate leaves, whereas *F. macropetala* is extremely similar to *F. macrophylla*, differing mainly in its longer flowers and fruits. Both these species grow close by in the Cordillera Azul near the Loreto-Huánuco border, and despite their close similarity, no intermediate forms have been observed.

Fuchsia macrophylla is isolated from other species in the section by its low altitudinal range. It is the lowest elevation species in Peru and enters into the subtropical vegetation zone. Much of this formation has been destroyed on the eastern slopes of the Andes, and this species was probably much more common until the recent increase in habitat destruction.

14. *Fuchsia macropetala* Presl, Rel. Haenk. 2:28. 1831. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):557. 1941. TYPE: Peru, Dept. Huánuco, in mountains of Huánuco, 1790, *Thaddeus Haenke* (PR 495859, holotype; photograph, MO). Although no definite locality information is given, Haenke visited the Cordillera Azul in 1790 (Kühnel, 1960), where he might have collected this specimen.

Erect to scandent shrubs 1.5–3 m tall. Young growth minutely puberulent; older branches glabrescent, with finely-splitting, tan brown bark. Leaves opposite, firmly membranous, elliptic, mostly acute at the base, acute to shortly acuminate at the apex, (7–)9–18 cm long, (3–)4–8 cm wide, subglabrous to strigillose on both surfaces, sometimes purple flushed below; secondary veins 13–18 on either side of the midvein, often reddish, prominent below and anastomosing into

a submarginal vein; margin subentire. Petiole subglabrous, 6–16 mm long. Stipules lanceolate to triangular, sometimes connate, 1–2 mm long, ca. 0.7 mm wide, mostly deciduous. Flowers few to many in lateral racemes or on short side branchlets 1–6(–10) cm long. Pedicels subglabrous, 9–26 mm long, reddish. Ovary ellipsoid, 6–8 mm long, ca. 3 mm thick, light green, finely strigillose and $\pm$ verrucose. Floral tube subcylindric, 32–45 mm long, 2.5–3 mm wide at the base, slightly constricted to ca. 2 mm wide above the nectary and gradually widened above until 5–7 mm wide at the rim, finely strigillose outside, pilose inside in lower $\frac{1}{2}$. Sepals lanceolate, 10–13 mm long, 3–5 mm wide, spreading at anthesis. Tube and sepals bright red. Petals red, elliptic-oblong, 10–12 mm long, 4–6 mm wide. Nectary mostly unlobed, 1–1.5 mm high. Filaments red, 7–10 mm and 5–8 mm long; anthers oblong, ca. 2 mm long, ca. 1 mm wide. Style pubescent for most its length, red; stigma capitate, ca. 2 mm long, 2–4 mm wide, slightly 4-cleft apically, dull white to pink, exserted 4–10 mm beyond the anthers. Berry ellipsoid, 15–18 mm long, 7–10 mm thick, dull dark purple; seeds 1.5–2 mm long, dull dark purple; seeds 1.5–2 mm long, 0.9–1.2 mm wide.

Distribution: Central Peru. Known only from the Cordillera Azul, which is a semi-isolated Andean spur to the east of the main Andean cordilleras of Peru and which runs along the Huánuco-Loreto border before joining the main cordillera in southern Huánuco. Clearings and roadsides, 1,600–1,800 m (Fig. 56).

Specimens examined: PERU, HUÁNUCO: 37 km E of Tingo María, near ridge of La Divisoria, *Berry & Aronson* 3089 (MO, USM), 3090 (MO, USM), 3090-B (MO); La Divisoria, *Gentry et al.* 18880 (MO); Cuchero, 9°35'S, 75°45'W, *Poeppig* 1081 (BM, W), *s.n.* (W 2 sheets); Km 194, La Divisoria, *Ridoutt s.n.* (*Vargas* 4654) (CUZ), *USM* 13004 (MO, USM). LORETO: Divisoria, 59 km from Tingo María, *Allard* 21226 (RSA, US), 21297 (RSA, US); just E of crest at La Divisoria, *Berry & Aronson* 3091 (MO); near Divisoria, *Ferreyra* 991 (GH, MO, NY, RSA, US, USM); 2244 (MO, US, USM), *Smith & Vera* 364-H-E (RSA). WITHOUT LOCALITY: *Poeppig* 156 (G, LE, P); *Poeppig s.n.* (LE).

This is the only species with lateral inflorescences (Fig. 40) and floral tubes more than 32 mm long. It is closely related to *F. macrophylla*, which shares the same low altitude distribution, lateral inflorescences, and large, elliptic leaves. *Fuchsia macrophylla* has shorter flowers with green sepal tips and smaller, rounder berries, however. These are the only species of *Fuchsia* known from the low Cordillera Azul, but it is not known if the two grow together. Further field study will be required to determine how these closely related species are isolated or if any intermediates occur.

- 15. *Fuchsia ovalis*** Ruiz & Pavón, Fl. Peruv. Chil. 3:87, pl. 324, fig. a. 1802. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):560. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:64, pl. 10, fig. 54. 1943. TYPE: Peru, Dept. Huánuco, near Muña, 1778–1788, *Hipólito Ruiz & José Pavón* (MA 11/87, lectotype, here designated; photograph, MO). There are also four other Ruiz and Pavón sheets of this species at MA, two at BM, and one each at F, G, MO, and NY, but these lack label information and may not be part of the same collection set.

Fuchsia polyanthella I. M. Johnston, Contr. Gray Herb. 75:36. 1925. TYPE: Peru, Dept. Huánuco, Muña, trail to Tambo de Vaca, ca. 2,700 m, 5–7 June 1923, *Francis Macbride* 4290 (F 535372, holotype; photographs, NY, UC; GH, K, isotypes).

Erect to scandent shrubs 1–3 m tall. Young leaves and shoots mostly densely pilose; older branches pilose to glabrescent, 5–13 mm thick, with light tan, finely fissured bark. Leaves opposite to quaternate, firmly membranous, broadly elliptic to ovate, rounded to acute at the base, acute to short acuminate at the apex, mature leaves 8–16 cm long, 3–7.5 cm wide, dark green and strigose above, paler green and strigose-pilose below, especially along the veins; secondary veins 14–17 on either side of the midvein, emerging from the midvein at $\pm 90^\circ$ and becoming gradually incurved towards the margin, anastomosing into a submarginal vein; margin subentire to obscurely denticulate. Petioles pilose, 2–7 cm long, reddish. Stipules lanceolate on young nodes, often triangular, connate, and recurved on older stems, 2–4 mm long, 2–3.5 mm wide. Flowers several to numerous in lateral racemes or panicles; rachis 5–10 cm long; bracts narrowly lanceolate, long acuminate, pilose, 6–12 mm long. Pedicels pilose, $\pm$ divergent, 10–20 mm long. Ovary cylindrical, 5–7 mm long, ca. 2 mm thick, loosely pilose. Floral tube narrowly funnelform, 18–20 mm long, ca. 2 mm wide and slightly bulbous at the base, gradually widened above until 3–4.5 mm wide at the rim, sparsely pilose outside, densely retrorse villous inside in lower $\frac{1}{2}$. Sepals lanceolate, acuminate, 10–13 mm long, 3–3.5 mm wide, usually noticeably longer than the petals, with tips forming a point ca. 2 mm long in bud. Tube and sepals red. Petals red, oblong, acute, 5–9 mm long, ca. 3 mm wide. Nectary shallowly 4-lobed, ca. 1.2 mm high. Filaments light red, 5–6 mm and 3–4 mm long; anthers oblong, ca. 2 mm long, ca. 1 mm wide. Style glabrous, reddish; stigma capitate, ca. 3 mm long, ca. 2 mm wide, slightly 4-cleft apically, exserted 2–3 mm beyond the anthers. Berry cylindrical or ellipsoid, 12–13 mm long, ca. 6 mm thick, subtetragonous, red purple; seeds 0.9–1.1 mm long, ca. 0.7 mm wide.

Distribution: Central Peru. Restricted to Depts. Huánuco, Pasco, and Junín, rare in cloud forest thickets; 2,000–2,800 m (Fig. 56).

Specimens examined: PERU, HUÁNUCO: Muña, *Lobb 114* (K), *Pearce 511* (K), *Weberbauer 6721* (F); Chinchao, *Ruiz & Pavón s.n.* (BM); Saraypampa, *Woytkowski 34193* (F, UC); Huamincha, *Woytkowski in 1946* (USM). JUNÍN: Chuquishuinca, 2 km above Huacapistana, between Tarma and San Ramón, *Ferreyra 454* (MO, USM); San Juan, near Huacapistana, *Ferreyra 11031* (MO); Vitoc, *Martinet 1585 bis* (P); above Huacapistana, *Sandeman in 1938* (K); WITHOUT LOCALITY: *Lobb s.n.* (K 2 sheets); *Pearce s.n.* (BM).

This species is easily recognized by its large, broad, long-petiolate leaves and densely pilose pubescence on the leaves and flowers. The leaves, bracts, pubescence, and flower size are similar to those of *F. pilosa*, but it is placed with *F. macrophylla* and *F. macropetala* in the same species group because of its lateral inflorescence.

Fuchsia ovalis is rare, and the most recent collection is from 1955 in a now deforested area (the Chanchamayo valley). Because of this, its sympatric occurrence with other species is unknown.

16. ***Fuchsia pilosa*** Fielding & Gardner, Sert. Pl. t. 27. 1844. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):561. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:65. 1943. TYPE: Peru, Dept. Amazonas, Taulia, S of Molinopampa, 1835–1841, *Andrew Mathews 1492* (OXF, holotype; photograph, MO; BM, CGE, K 2 sheets, isotypes).

Fuchsia asperifolia K. Krause, Repert. Spec. Nov. Regni Veg. 1:169. 1905. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):547. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:65. 1943. TYPE: Peru, Dept. Amazonas, between Tambos Bagazán and Almirante, E of Chachapoyas on path to Moyobamba, 2700 m, 1904–1921, August Weberbauer 4445 (B, holotype, destroyed in World War II; photograph, F).

Shrub 1–2 m tall with densely hirsute young growth, the hairs usually whitish, shaggy, erect, 1.0–1.6 mm long; older branches glabrescent, with light tan, finely striated bark. Leaves opposite to quaternate, usually ternate, membranous, narrowly to broadly elliptic or oblanceolate, acute to attenuate at the base, acute to acuminate at the apex, 5–16 cm long, 2–7 cm wide, matte green and subglabrous to villous on upper surface, slightly paler and villous below; secondary veins 10–12 on either side of the midvein, sulcate above and prominent below, margin subentire. Petioles hirsute, 12–60 mm long. Stipules ca. 1 mm thick, prominent, lanceolate to triangular, 3–4 mm long, ca. 2 mm wide, often connate and recurved on lower nodes, persistent. Flowers numerous and crowded at the tips of terminal, drooping racemes; rachis 3–20 cm long; bracts narrowly lanceolate, 5–15 mm long. Pedicels slender, 3–5 mm long, ca. 1.5 mm thick. Floral tube narrowly funnelform, 16–20 mm long, slightly bulbous and ca. 2 mm wide at the base, gradually widened above until 4–5 mm wide at the rim, sparsely to moderately hirsute outside, densely retrorse villous inside in lower ½. Sepals lanceolate, long acuminate, 6–8 mm long, 2.5–3 mm wide, with free, divergent tips 2–3 mm long in bud, divergent with recurved tips at anthesis. Tube and sepals bright orange red. Petals orange red, delicate, oblong-elliptic, 6–8 mm long, 3–4 mm wide, recurved at anthesis. Nectary unlobed, ca. 1 mm high. Filaments orange red, 4–5 mm and 2–3 mm long; anthers oblong, 1.5–2 mm long, ca. 1 mm wide, white. Style glabrous, light red; stigma capitate, subtetragonous, 4-cleft apically, 1.5–2 mm long, 2–3 mm wide, dull white, exserted 1–2 mm beyond the anthers. Berry ellipsoid-oblong, 4-sulcate before maturity, 15–19 mm long, 10–12 mm thick, sparsely hirsute, reddish; seeds tan, ca. 1.5 mm long, 0.9–1.0 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Endemic to mid-elevation cloud forest in the mountains E of the Río Utcubamba in Dept. Amazonas; 1,600–2,400 m (Fig. 56).

Specimens examined: PERU, AMAZONAS: 9–11 km E of Molinopampa on Chachapoyas-Mendoza road, Berry & Escobar 3618 (MO, USM), 3619 (MO, USM), 3620 (MO, USM); above Pomacocha, Ferreyra 15170 (MO); Tresleras, on Pomacocha-Yambrasbamba trail, Ferreyra 15233 (MO); Almirante, Mathews 1481 (K), Sandeman 54 (K, OXF); mountains S of Tambo de Ventilla, Pennell 15794 (USM); Mendoza, Woytkowski 8202 (MO), 8325 (US).

This is one of several species endemic to Dept. Amazonas in northern Peru. It is most easily recognized by its stiff, hirsute pubescence, broad leaves, and terminal, drooping inflorescence of red orange, short-pedicellate flowers. Because of floral and foliar similarities to *F. ovalis*, it is placed in the *F. macrophylla* species group, but in its abrupt, terminal inflorescences and thick, persistent stipules it resembles other species such as *F. wurdackii* and *F. glaberrima*.

Fuchsia pilosa grows together with *F. rivularis* in cloud forest thickets in Dept. Amazonas. No hybrids or intermediates were found between them, which is at least partly due to differences in habit. Although their basal stems may at times be entangled, *F. pilosa* persists as a low, upright shrub with dangling inflo-

rescences, while *F. rivularis* is a scandent-climbing species with long branches and subaxillary flowers that are usually found higher above ground than *F. pilosa*.

17. ***Fuchsia putumayensis*** Munz, Proc. Calif. Acad. Sci. IV. 25:62, pl. 8, fig. 52. 1943. TYPE: Colombia, Com. Putumayo, Mocoa, 23 May 1935, *Hernando García-Barriga* 4639 (US 1593482, holotype; photographs, NY, POM, UC; AAU, COL, isotypes).

Shrubs or subshrubs 1–3 m high. Young growth minutely puberulent; branchlets terete, 2–5 mm thick, green to dull purple; older stems pale tan gray, with finely fissured bark. Leaves opposite, firmly membranous, elliptic, rounded to acute at the base, acute to subacuminate at the apex, 6–15 cm long, 3–7 cm wide, matte green and glabrous above, pale green and subglabrous to finely puberulent below along the subelevated nerves; secondary veins 9–13 on either side of the midvein, impressed above; margin subentire. Petioles 6–15 mm long, puberulent to subglabrous. Stipules lance-deltoid, thick at the base and subulate at the apex, occasionally connate, 1–2 mm long, 0.4–0.8 mm wide, deciduous. Flowers numerous in mostly compact, terminal and subterminal racemes; rachis 1–4(–10) cm long; bracts lance-linear, 10–25 mm long, $\pm$ recurved, often deciduous. Pedicels slender, divergent, puberulent, 8–25 mm long. Ovary oblong, 4–5 mm long, 1.5–2 mm thick, puberulent, reddish. Floral tube narrowly funnelform, 15–27 mm long, 2–2.5 mm wide at the base, slightly constricted to 1.5–2 mm wide above the nectary, gradually widened above until 4–7 mm wide at the rim, finely puberulent outside, pubescent inside in the lower $\frac{1}{3}$. Sepals lanceolate, acuminate, 8–11 mm long, 3–5 mm wide, with a 1.5–2 mm long tip in bud, divergent at anthesis. Tube and sepals nitid orange to coral red. Petals orange red, delicate, elliptic-oblong, 6–9 mm long, 3–4 mm wide, obtuse or mucronate at the apex, somewhat erose-margined, strongly spreading and recurved at anthesis. Nectary unlobed, 1–1.2 mm high, ca. 0.8 mm thick. Filaments orange red, 4–6 mm and 2.5–4 mm long; anthers elliptic-oblong, 1.5–2.3 mm long, ca. 1 mm wide, cream. Style glabrous, light red; stigma subglobose, slightly 4-lobed apically, cream to pink, exserted shortly above the anthers. Berry oblong-ellipsoid, 10–12 mm long, 5–9 mm thick, subnitid red purple; seeds tan, 1–1.2 mm long. 0.6–0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia and Ecuador. Low cloud forest shrubs in the Cordillera Occidental of Colombia from Antioquia to Valle, and on the eastern slopes of the Cordillera Central and Cordillera Oriental in Colombia and Ecuador from Cauca south to Napo; 1,400–2,100 m (Fig. 58).

Specimens examined: COLOMBIA, ANTIOQUIA: trail Encarnación-Parque Nacional Las Orquídeas, *Gentry & Rentería* 24607 (MO). CAUCA: Río Villalobos, vicinity of Río Sauzita, *Schultes & Villarreal* 5156 (COL, GH), 5173 (F, GH). CHOCÓ: 53–55 km W of Ansermanuevo on road to San José del Palmar, *Berry* 3561 (COL, MO), 3562 (COL, MO), 3563 (COL, MO); Km 120–135 of Tutunendo-El Carmen road, alto Río Atrato, *Forero et al.* 6172 (MO); Quebrada El Sucio, above Carmen de Atrato, *Fosberg & Core* 21551 (RSA, US); 11 km E of San José del Palmar, *Luteyn et al.* 7328 (COL, MO NY). PUTUMAYO: Planada de Minchoy, between Sachamates and San Francisco de Sibundoy, *Cuatrecasas* 11436 (COL, F, US); between Sachamates and San Antonio, *Ewan* 16684 (COL, F, POM, US); Km 128 from Pasto to Mocoa, *Plowman & Davis* 4406 (COL, PSO). RISARALDA: Pueblo Rico, *von Sneider* 5464 (F, RSA, S, US), 5546 (COL, MICH, RSA, S, US). VALLE: "Tokio," above El Queremal,

Berry 3564 (COL, MO); Quebrada Robada, Alto Bonito, drainage of Río Albán, *Cuatrecasas* 22323 (F, RSA, VALLE); Quebrada of Río San Juan, above El Queremal, *Cuatrecasas* 23933 (F, RSA); Calima valley, *Hugh-Jones* 445 (COL, K, US); *Langlassé 60 bis* (G 2 sheets). ECUADOR, NAPO: Cerro Antisana, forest E of Borja, *Grubb et al.* 1083 (K, NY); Borja, *Harling* 3871 (NY, S); 16.5 km NNE of Santa Rosa, road Baeza-Lago Agrio, *MacBryde* 728 (MO); junction Baeza-Lago Agrio road with Río Azuela, *MacBryde* 808 (MO, QCA); 28 km E of Baeza, before Salado, *Plowman et al.* 3951 (COL, F, GH, MO, S).

This species is part of a group with *Fuchsia lehmannii*, *F. andrei*, and *F. cuatrecasasii* that have flowers usually tightly grouped in short terminal inflorescences with lanceolate or deciduous bracts and $\pm$ divergent pedicels. *Fuchsia putumayensis* has uniformly elliptic, opposite leaves like *F. cuatrecasasii*, but shorter, orange flowers with somewhat erose petals as in *F. lehmannii*.

Like *F. pallescens*, this species is disjunct from the western slopes of the Cordillera Occidental in Colombia to the eastern slopes of the Andes in Ecuador and Colombia. Most Ecuadorian populations have longer racemes (ca. 10 cm long) than most collections from Colombia, but occasional Colombian specimens such as *Langlassé 60 bis* (G), from Valle, also have loose inflorescences.

Although *F. putumayensis* is the lowest elevation fuchsia in the northern Andes and is generally altitudinally separated from other species, a probable hybrid with *F. nigricans* (*Robinson 138*, K) was found and is discussed under that species.

- 18. *Fuchsia lehmannii* Munz**, Proc. Calif. Acad. Sci. IV. 25:61, pl. 9, fig. 51. 1943; Opera Bot., Ser. B, 3:17. 1974. TYPE: Ecuador, Prov. Morona-Santiago, east Andes of Sigisig, 1,600–1,800 m, 1850–1903, *Friedrich C. Lehmann* 5498 (F 550994, holotype; photographs, MO, NY, POM, UC; GH, K, US, isotypes).

Scandent to erect shrubs 1–3 m tall, mostly with numerous short lateral branches 5–12 cm long near the tips of the main stems. Leaves 2–4 per node, mostly ternate or quaternate, membranous, narrowly (ob-)lanceolate to narrowly elliptic, acute to acuminate at the base, acuminate at the apex, 4–11(–15) cm long, 1–3.5(–4.2) cm wide, subnitid dark green and glabrous above, pale green and glabrous or pubescent along veins below; secondary veins 8–10(–11) on either side of the midvein, impressed above, margin entire. Petioles 4–12(–20) mm long, subglabrous to strigillose, mostly reddish. Stipules lanceolate, 1.5–2 mm long, 0.4–0.8 mm wide, deciduous. Flowers numerous in compact, terminal and subterminal racemes; rachis 0.5–3 cm long, usually $\pm$ strigose; bracts narrowly lanceolate, acuminate, usually reflexed, 5–15 mm long, 1–4 mm wide. Pedicels slender, 8–15 mm long, $\pm$ divergent, strigose or glabrous. Ovary oblong, 3–5 mm long, 1.5–2.5 mm wide, subglabrous, mostly wine red. Floral tube narrowly funnelform, 22–35 mm long, 1.5–2.5 mm wide and slightly bulbous at the base, narrowed to 1.2–2 mm wide for the basal $\frac{1}{3}$, then dilated to 6–9 mm wide before narrowing slightly towards the rim of the tube, glabrous outside, pilose inside in basal $\frac{1}{3}$. Sepals narrowly lanceolate, 10–13 mm long, 2.5–4 mm wide, generally long acuminate, 4-angled in bud with a tip 2–3 mm long, strongly divergent to slightly reflexed at anthesis. Tube and sepals nitid orange to coral red. Petals delicate, orange red, narrowly lance-oblong, 8–11 mm long, 2.5–4 mm wide, acute at the tip, undulate and spreading-reflexed at anthesis. Nectary unlobed, ca. 1 mm high.

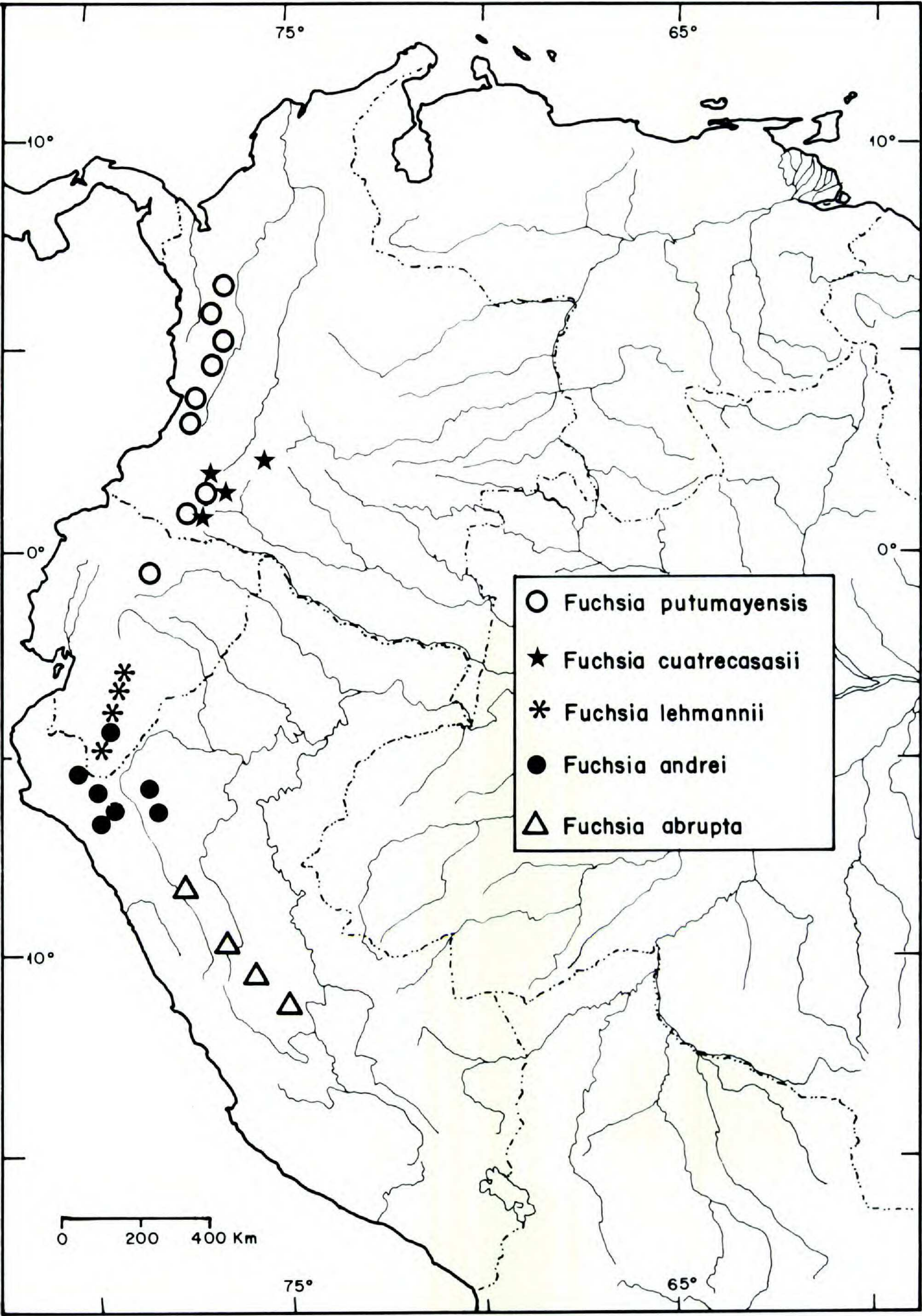


FIGURE 58. Distribution of the *Fuchsia putumayensis* species group.

Filaments orange red, 5–6 mm and 3–4 mm long; anthers oblong, 1.5–2 mm long, 1.1–1.3 mm wide, cream. Style orange red, mostly glabrous or loosely villous in lower ½; stigma capitate, shortly 4-cleft at apex, 2–2.5 mm long, ca. 2 mm wide, dull cream to orange red. Berry oblong-ellipsoid, 11–15 mm long, 7–8 mm thick, turning dark purple at maturity; seeds 0.9–1.1 mm long, 0.7–0.8 mm wide, brown. Gametic chromosome number $n = 11$.

Distribution: Southern Ecuador. Moist thickets, streamsides, and roadbanks on the eastern slopes of Prov. Zamora-Chinchipe and Morona-Santiago; 1,600–2,250 m (Fig. 58).

Representative specimens examined: ECUADOR, MORONA-SANTIAGO: Tambo Chontal to Tambo Consuelo, slopes above Ríos Negro and Chupianza, Seville de Oro trail, *Camp E-1589* (NY, RSA). ZAMORA-CHINCHIPE: 27 km E of Loja to Zamora, *Berry & Escobar 3200* (MO, QCA); Hacienda Montecristi, ca. 40 km NE of Loja, *Espinosa E-1461* (US); Canillones, Río San Francisco, *Fosberg 23165* (COL, NY, RSA, US); 5 km W of Tambo, Loja-Zamora road, *Harling 5865* (NY, S); Km 39 Loja-Zamora road, *Holm-Nielsen et al. 4066* (AAU, COL, MO, NY, S); Km 33 Loja-Zamora road, *Holm-Nielsen et al. 4134* (AAU, COL, MO, NY, S); Río Savonilla, *Lehmann 7858* (F, K, US); below El Retorno, *Mathias & Taylor 5200* (F, RSA, USM); trail from Mirador to Pailas, *Steyermark 54281* (NY); Tambo Valladolid, *Steyermark 54654* (NY).

This species is most closely allied to *F. putumayensis* and *F. andrei*, both species with tight, many-flowered inflorescences of orange red flowers and delicate petals. It has narrower leaves than either of these species, however, longer sepals, and floral tubes that are widest below the rim of the tube. Although it has not been found sympatrically with other fuchsias, its altitudinal and geographical ranges overlap with those of *F. glaberrima* and *F. andrei*.

19. **Fuchsia andrei** I. M. Johnston, Contr. Gray Herb. 75:31. 1925. Munz, Proc. Calif. Acad. Sci. IV. 25:61, pl. 9, fig. 50. 1943. TYPE: Ecuador or Peru (locality uncertain), Río de Huarunamaca (as appears on K sheet, transcribed to "Río de Huannamaca" on the sheets at F and NY), 19 Nov. (?) 1876, *Édouard André K.820* (F 537131, holotype; photographs, MO, NY, POM, UC; K, NY, isotypes). I have been unable to find the above locality in maps or gazeteers of either Colombia, Ecuador, or Peru, where André collected in 1876. According to Johnston's protologue, the locality is from Colombia. A detailed list of André's itinerary, however, does not mention this river for either Colombia or Ecuador (Smith, 1965). The last part of André's itinerary in southern Ecuador and northern Peru was not included in Smith's list, however, and that is when André hired H. Poortman to collect for him (L. B. Smith, pers. comm.). Since André had already returned to Europe in Sept. 1876, this collection must have been made by Poortman, who collected mostly in Prov. Loja of southern Ecuador.

Fuchsia osgoodii J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):559. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:60, pl. 9, fig. 49. 1943. TYPE: Peru, Dept. Libertad, Uchco, 15 June 1912, *Wilfred H. Osgood & Mary P. Anderson 47* (F 346773, holotype; photographs, NY, UC).

Fuchsia ovalis var. *aberrans* J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):560. 1941. TYPE: Peru, Dept. Cajamarca, Prov. Cutervo, Arenales, S of San Tomás, 3,000 m, 12 Dec. 1938, *Harvey E. Stork & Ovid. B. Horton 10155* (F 1052360, holotype; photograph, NY; G, NA, UC, isotypes).

Shrubs 1–4 m tall. Branchlets terete, 3–8 mm thick, sparsely puberulent to strigillose; older stems 8–14 mm thick, with tan, finely striated bark. Leaves

opposite or less often ternate, membranous, (narrowly) elliptic to obovate, acute to cuneate at the base, subacuminate at the apex, (5–)7–17 cm long, 2–9(–11) cm wide, glabrous above, subglabrous to strigose below on midvein and along margin; secondary veins (8–)12–15 on either side of the midvein; margin entire or subdenticulate. Petioles 6–20(–30) mm long. Stipules triangular, dark, 1.5–2 mm long, ca. 1.5 mm wide, subpersistent. Flowers numerous in short, terminal and subterminal racemes; rachis 2–6 cm long; bracts lanceolate, 6–10 mm long, 2–4 mm wide. Pedicels slender, mostly strigose, $\pm$ divergent, (7–)10–18(–25) mm long. Ovary oblong, 5–6 mm long, 2–2.5 mm thick. Floral tube narrowly funnelform, 23–38(–45) mm long, 1.5–2 mm wide and subnodose at the base, narrowed to 1–1.5 mm in basal $\frac{1}{3}$, gradually widened above until 4–7 mm wide at the rim, glabrous outside, pilose inside in lower $\frac{1}{2}$. Sepals lanceolate, acute to subacuminate, (6–)8–13 mm long, 4–5 mm wide. Tube and sepals orange to coral red. Petals orange red, oblong, obtuse to acute at the apex, 7–12 mm long, 2.5–4 mm wide, nectary unlobed, ca. 1 mm high. Filaments light red, 6–8 mm and 4–6 mm long; anthers oblong, 1.5–2 mm long, 1–1.2 mm wide. Style light red, glabrous to pilose in lower $\frac{1}{2}$; stigma capitate, 4-cleft apically, 2–2.5 mm long, ca. 2.5 mm wide. Berry oblong-ellipsoid, 10–12 mm long, 6–8 mm thick, green to red; seeds tan, 1–1.2 mm long, 0.7–0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Ecuador and northern Peru. Cloud forest and semi-open moist scrub in Prov. Piura, Cajamarca, and Amazonas, Peru and in Prov. Zamora-Chinchipe, Ecuador (1,130–)1,800–3,000 m (Fig. 58).

Specimens examined: ECUADOR, ZAMORA-CHINCHIPE: Tambo de Savanilla, *André K.818* (F, GH, NY). PERU, AMAZONAS: Cordillera Colán SE of La Peca, *Barbour 3995* (MO), *4083* (MO); 13 km E of Molinopampa on Chachapoyas-Mendoza road, *Berry & Escobar 3621* (MO, USM); Km 42 of Carretera Marginal from Pedro Ruiz to Rioja, *Berry & Escobar 3628* (MO, USM); Prov. Bongará, *Ferreyra 15170* (MO 2 sheets), *15233* (MO); E side Cerros Calla-Calla, 5 km above Leimebamba, *Hutchison & Wright 4884* (UC); Río Almirante, *Sandeman in 1938* (K); Mendoza, *Woytkowski 8325* (US); 2–4 km WSW of Pomacocha, Prov. Bongará, *Wurdack 850* (US). CAJAMARCA: above Tabaconas, 18 km SE of Huancabamba, Prov. Jaen, *Fosberg 27835* (MO); Hacienda Taulis, vicinity of the Casa Hacienda, Prov. Hualgayoc, *Hutchison & Bismark 6326* (F, MICH, MO, NY, P, RSA, UC, US); San Andrés, Prov. Cutervo, *López & Sagástegui 5436* (MO, US), *Sagástegui in 1969* (NY), *Velarde Núñez 6971* (Z); Monte Seco, Prov. Hualgayoc, *Soukup 3848* (F, US). PIURA: Canchaque, *Stork 11428* (UC).

It is difficult to adequately circumscribe this species because the specimens available are from widely scattered localities throughout northern Peru and because it is not possible to determine the type locality. When more critical collections and field observations have been made in this area, the material treated below will probably be found to comprise several distinct taxa. They are grouped together here, however, because of their similar, compact racemes and generally short-tubed flowers with slender pedicels. In these characters, the specimens included under *F. andrei* are related to *F. lehmannii* and *F. putumayensis*. The type specimen and *Hutchison & Bismark 6326* are characterized by their large leaves ca. 16 cm long and ca. 10 cm wide. This and the somewhat narrower floral tubes distinguish them from *F. lehmannii* of southern Ecuador. There are a number of collections from other areas, though, that show the following differences:

Collections from Prov. Cutervo in Dept. Cajamarca. *López & Sagástegui 5436*, *Velarde Núñez 6971*, and *Sagástegui s.n.* have small, narrow leaves and floral tubes less than 25 mm long. *Stork & Horton 10155*, though, which Macbride

described as *F. ovalis* var. *aberrans*, has some larger, basal leaves that approach those of the type of *F. andrei*.

Stork 11428. This collection from Cajamarca has floral tubes 42–45 mm long and is recorded as growing at 1,130 m, which is much lower than the other specimens considered here. The area where it was collected has been severely altered, however, and no further populations were found when I visited the area in 1979.

Fosberg 27835. The leaves of this collection are narrowly elliptic as in *F. lehmannii*. The same is true for *Osgood & Anderson 47*, the type of *F. osgoodii*, but it has not been possible to identify the locality of this collection, believed by Macbride to be in Dept. Libertad.

Collections from Dept. Amazonas. These are considerably isolated from the specimens to the west of the Río Marañón, and they occur in wetter, cloud forest habitats. *Wurdack 850* and *Hutchison & Wright 4884* have short tubes just over 20 mm long and small, elliptic leaves with subdentate margins. *Woytkowski 8325* has broad leaves ca. 7 cm wide but similarly short flowers. *Ferreira 15233* has floral tubes 45 mm long. These wide differences suggest that several different entities might be involved in these collections, but further material is needed to determine their limits.

- 20. *Fuchsia cuatrecasasii* Munz**, Proc. Calif. Acad. Sci. IV. 25:51, pl. 7, fig. 40. 1943; non Munz, Opera Bot., Ser. B, 3:14. 1974. TYPE: Colombia, Com. Caquetá, Cordillera Oriental, E slopes, Quebrada del Río Hacha, open woods in Cajón de Pulido, 1,700 m, 26 March 1940, *José Cuatrecasas 8738* (US 1796401, holotype; photographs, MO, NY, POM, UC; COL, isotype).

Subshrubs 0.5–1.5 m high. Branchlets terete to slightly flattened, 2–6 mm thick, subglabrous, green to reddish purple; older branches with light tan-gray bark. Leaves opposite, elliptic, firmly membranous, acute at both ends, smooth and glossy above, subglossy and finely strigillose below on veins and margins; secondary veins 8–12 on either side of the midvein, $\pm$ impressed above, at times purple tinged below; margin subentire. Petioles stout, sparsely strigose, 4–14(–17) mm long, red purple. Stipules triangular, firm, dark purple, 1–2 mm long, ca. 1.5 mm wide, subpersistent. Flowers few to many in a compact, terminal, drooping raceme; rachis 1–5(–8) cm long; bracts lanceolate, 8–18 mm long, reflexed. Pedicels 7–13 mm long. Ovary oblong, 4–7 mm long, 1.5–2.5 mm thick, strigillose, subnitid red purple. Floral tube narrowly funnelform, (28–)35–50(–55) mm long, slightly nodose and 2–3.5 mm wide at the base, narrowed to 1.5–3 mm wide in lower $\frac{1}{3}$ and widened above until 6–8 mm wide at the rim, puberulent outside, pubescent inside in lower $\frac{1}{3}$. Sepals lanceolate, acuminate, (8–)10–20 mm long, 4–6 mm wide, tips usually free in bud for 2–4 mm. Tube and sepals nitid red to orange red. Petals orange red, elliptic to oblanceolate, 9–15 mm long, 4–6 mm wide, acute at the apex, spreading at anthesis. Nectary unlobed, ca. 1.5 mm high. Filaments orange red, 5–9 mm and 4–5 mm long; anthers oblong, 2–3 mm long, 1–1.5 mm wide. Style sparsely villous in lower $\frac{1}{2}$, orange red; stigma capitate, tetragonous, 4-lobed in upper $\frac{1}{2}$, 2–3 mm long, 2–3 mm wide, cream, exserted 1–4 mm beyond the anthers. Berry ellipsoid, 15–20 mm long, 10–15 mm thick, lustrous red purple; seeds 1.1–1.3 mm long, 0.6–0.8 mm wide.

Distribution: Colombia. Infrequent, low shrubs in moist, open thickets in cloud forest on eastern slopes of the Andes from Caquetá south to Putumayo, 1,400–2,200 m (Fig. 58).

Specimens examined: COLOMBIA, CAUCA: Río Villalobos, between the junction of the Ríos Villalobos and Cauchos, *Schultes & Villarreal* 5203 (COL, DS, F, GH, MO, UC, US). HUILA: Km 31 of Pitalito-Mocoa road, *Berry* 3594 (COL, MO); Km 28–32 of Pitalito-Mocoa road, near divide, *Luteyn et al.* 7538 (COL, MO, NY). PUTUMAYO: Mirador, between San Francisco and Mocoa, *Bristol* 542 (COL, DS); between El Silencio and La Cabaña, road from Sibundoy to Urcusique, *Cuatrecasas* 11495 (COL, US); Cordillera del Portachuelo, road Sibundoy-Mocoa, *García-Barriga et al.* 18635 (COL); El Mirador, San Francisco-Mocoa, *Idrobo & Ospina* 2364 (COL); Km 90–91 between Sibundoy and Mocoa, *Luteyn et al.* 5043 (COL, MO, NY); San Francisco to Mocoa, *Mora* 3440 (PSO), 4460 (COL), *Schultes & Cabrera* 18625 (RSA); Km 112 from Pasto to Mocoa, *Plowman & Davis* 4348 (COL, PSO); Punto Buenos Aires, Cerro Portachuelo, *Soejarto* 1125 (GH, PSO).

The short, terminal racemes of tightly packed flowers in *F. cuatrecasasii* is of the same type found in *F. putumayensis*, *F. lehmannii*, and *F. andrei*. Its flowers are considerably longer than these species, however, and the leaves are uniformly elliptic, opposite, glossy, firm, and short-petiolate. Vegetatively, *F. putumayensis* is the most closely related species. *Fuchsia cuatrecasasii* occurs sympatrically with *F. putumayensis*, *F. scabriuscula*, *F. sessilifolia*, and *F. verrucosa*, but it is rare, and no apparent hybrids have been detected.

- 21. *Fuchsia abrupta*** I. M. Johnston, Contr. Gray Herb. 75:37. 1925. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):545. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:50, pl. 7, fig. 39. 1943; non Opera Bot., Ser. B, 3:10. 1974. TYPE: Peru, Dept. Pasco, along river at Cushi, ca. 1,500 m, 19–23 June 1923, *Francis Macbride* 4541 (F 535618, holotype; photographs, NY, POM, UC; GH, K, US, isotypes). Fig. 20.

Fuchsia aspiazui J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):547. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:43, pl. 6, fig. 31. 1943. TYPE: Peru, Dept. Libertad, Prov. Pataz, valley of the Río Mixiollo, Aug. 1914, *August Weberbauer* 7042 (F 629319, holotype; photographs, NY, UC; F 2 sheets, GH, US, isotypes).

Scandent to erect shrubs 1–3 m tall. Young branches semisucculent, terete, 3–6 mm thick, subglabrous to densely hispid; older stems 8–15 mm thick, light tan with finely fissured bark. Leaves opposite or ternate, firmly membranous, narrowly to broadly elliptic or (ob-)ovate, acute at the base, acute to acuminate at the apex, 7–14(–19) cm long, 3–6(–10) cm wide, subnitid dark green and sparsely strigose to subglabrous above, pale and strigose to densely villous or hispid below, especially along the veins; secondary veins 15–22 on either side of the midvein, strongly impressed above, anastomosing into a distinct submarginal vein; margin subentire to obscurely denticulate. Petioles strigose, 4–10 mm long. Stipules conspicuous, dark, (narrowly) triangular, sharply acute-tipped, 3–6 mm long, 2–3 mm wide, often connate, persistent. Flowers few to numerous and usually verticillately disposed in terminal, arching racemes; rachis (8–)10–35 cm long, elongating in fruit; bracts lanceolate, divergent, 15–45 mm long. Pedicels spreading at anthesis and 10–15 mm long, divergent and ascending in fruit, when 15–35 mm long, light red. Ovary cylindric, 7–9 mm long, ca. 2 mm thick, lustrous light red, the ovary or floral tube usually somewhat deflexed so that the distal portion of the flower is pendant. Floral tube narrowly funnelform, 35–50(–60) mm

long, 2.5–3.5 mm wide and bulbous at the base, constricted to ca. 2 mm wide for the basal 5–8 mm of the tube, gradually widened above until 6–10 mm wide at the rim, glabrous outside, densely pilose inside in basal $\frac{1}{3}$. Sepals lanceolate, 13–20 mm long, 4–7 mm wide, mostly long acuminate at the apex, cuspidate and tetragonous in transection in bud, conspicuously wider than the rim of the tube, divergent at anthesis. Tube and sepals nitid, bright orange red. Petals orange red, delicate, oblong, round to acute at the apex, 13–19 mm long, 5–7 mm wide, spreading to divergent at anthesis with the apical portion recurved and the margins undulate. Nectary green, shallowly 4-lobed, 2.5–3 mm high and ca. 0.7 mm thick. Filaments orange red, 8–10 mm and 6–7 mm long; anthers oblong, 2.5–3 mm long, ca. 1.5 mm wide, white. Style pale red, glabrous; stigma capitate, 2–3 mm long, 2–3 mm wide, 4-cleft apically, pale red. Berry cylindrical-ellipsoid, 18–22 mm long, ca. 10 mm thick, purplish; seeds tan, 1.1–1.4 mm long, 0.8–1.0 mm wide. Gametic chromosome number $n = 11$.

Distribution: Central Peru. Scattered shrubs in cloud forest thickets on the eastern slopes of the Andes from Depts. Libertad to Junín, 1,500–2,700 m (Fig. 58).

Representative specimens examined: PERU, HUÁNUCO: Carpish, *Ferreyra* 1719 (MO, RSA, US, USM); Carpish, above Acomayo, *Hutchison et al.* 5920 (F, NY, RSA, UC, USM); above Chinchao towards summit of Carpish, *Mathias & Taylor* 4033 (F, RSA, USM); Tumanga, *Woytkowski* 7951 (US). JUNÍN: 57–58 km above Satipo on road to Concepción, *Berry & Aronson* 3077 (MO, USM), 3078 (MO); Km 175 Satipo-Concepción, *Seibert* 2379 (MO, POM, US). PASCO: Pozuzo, *Pearce* 537 (K).

Fuchsia abrupta is distinguished by its noticeably veiny leaves (due to the numerous, impressed secondary veins), large, persistent stipules, and long, terminal inflorescences with divergent to ascending pedicels and cylindrical fruits. Its affinities are unclear, but despite its elongate racemes, it is placed in the *F. putumayensis* species group because of its divergent pedicels, orange flowers with delicate petals, and narrowly lanceolate bracts. In dried specimens, it may be confused with *F. corymbiflora*, but that species has finely puberulent leaves, rounder fruits, and shorter racemes and pedicels.

The specimen described as *F. aspiazui* has non-apiculate buds and unusually large leaves, but it has the same characteristic inflorescence and vegetative traits of *F. abrupta*. *Sandeman* 4503 (K; Peru, Dept. Junín above Huacapistana, ca. 2,000 m, Oct. 1943) is like *F. abrupta* in all characters except its much shorter floral tubes (17 mm long). *Sandeman* 4585 (K, OXF) from the same locality, is morphologically intermediate and is probably a hybrid with *F. decussata*. It is discussed further under that species. *Fuchsia abrupta* also occurs sympatrically with *F. ceracea*, *F. corymbiflora*, *F. denticulata*, and *F. ferreyrae*.

- 22. *Fuchsia petiolaris*** Humboldt, Bonpland & Kunth, Nov. Gen. Pl. 6:104. 1823. Munz, Proc. Calif. Acad. Sci. IV. 25:34. 1943. *Fuchsia petiolaris* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25:35, pl. 4, fig. 21. 1943. Based on *F. petiolaris* HBK. TYPE: Colombia, Dept. Cundinamarca, near Bogotá, ca. 2,500 m, July–Sept. 1801, *Alexander von Humboldt & Aimé Bonpland* (P, holotype, not seen; photograph, F; microfiche, MO).

Fuchsia quinduensis Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 6:105. 1823. TYPE: Colombia, Dept. Tolima or Quindío, in the Quindío Andes, ca. 2,500 m, Sept.–Dec. 1801, *Alexander von Humboldt & Aimé Bonpland* (P, holotype, not seen; photograph, F; microfiche, MO).

Fuchsia curviflora Benth., Pl. Hartw. 177. 1845. TYPE: Colombia, Dept. Cundinamarca, in Andes near Bogotá, ca. 3,000 m, 1841–1843, *Theodor Hartweg* (K, holotype).

Fuchsia smithii Munz, Proc. Calif. Acad. Sci. IV. 25:36, pl. 4, fig. 21. 1943. TYPE: Colombia, Dept. Santander, vicinity of Vetás, 3,200–3,250 m, 16–20 Jan. 1927, *Ellsworth Killip & Albert C. Smith* 17300 (GH, holotype; photograph, UC; A, F, NY, US, isotypes).

Fuchsia petiolaris var. *bolivarensis* Munz, Proc. Calif. Acad. Sci. IV. 25:35, pl. 4, fig. 22. 1943. TYPE: Colombia, Dept. Antioquia ("Bolivar" on Pennell's label), below Páramo de Cháquiro, Cordillera Occidental, 2,800–3,100 m, 24 Feb. 1918, *Francis W. Pennell* 4324 (NY, holotype; photographs, GH, POM, UC). The leaves of this collection are quite slender, but are within the range of those of *F. petiolaris*.

Low shrubs 0.5–2 m tall or climbing-scandent in trees to 5 m above ground. Young growth puberulent to pilulose; branchlets terete, 1.5–3 mm thick, puberulent to ferrugineous-pilose, green to light red purple; older branches 5–12 mm thick, with reddish tan, exfoliating bark. Leaves mostly ternate, up to 6 per whorl, firmly membranous to subcoriaceous, narrowly lanceolate to elliptic or obovate, acute to narrowly cuneate at the base, mostly acute at the apex, (1.5–)3–9(–11) cm long, (0.5–)1–3(–4.5) cm wide, medium to dark matte green and glabrous to puberulent above, pale green and subglabrous to puberulent or pilose below; secondary veins (4–)6–10(–11) on either side of the midvein; margin denticulate to serrulate or rarely subentire. Petioles (2–)5–20 mm long. Stipules lance-linear, 2–3 mm long, ca. 0.5 mm wide, subpersistent. Flowers few to many, axillary. Pedicels pendant, (10–)15–40(–55) mm long. Ovary ovoid, 5–8 mm long, 2–2.5 mm thick. Floral tube narrowly funnelform until the slightly constricted apex, (30–)35–50(–62) mm long, 2.5–4(–6) mm wide and somewhat bulbous at the base, narrowed to 1.5–3(–5) mm wide in the lower $\frac{1}{3}$ of the tube, then gradually to rather abruptly widened until (5–)6–11(–12) mm wide at the rim, strigillose to puberulent outside, pilose inside for most of length. Sepals ovate-lanceolate, conspicuously flared outwards from the tube at the base and 1–3 mm wider in bud than the rim of the tube, acute to acuminate, 11–23 mm long, (4–)6–8(–9) mm wide, with coherent or spreading tips in bud and the lobes sometimes splitting open in the middle before anthesis, spreading-divergent at anthesis, at times the basal $\frac{1}{2}$ divergent and the upper $\frac{1}{2}$ erect. Tube dull to subnitid rose pink, sepals usually paler, sometimes with greenish tips. Petals bright red pink, narrowly lanceolate to lance-elliptic, (narrowly) acute to rarely obtuse at the apex, (8–)12–16(–20) mm long, (4–)5–7(–8) mm wide, generally unguiculate at the base, margin smooth to occasionally serrulate, mostly with finely pubescent hairs over the dorsal surface or longer villous hairs along the midvein, rarely (sub-)glabrous, suberect at anthesis. Nectary green, unlobed or 4-lobed, 2–4 mm high. Filaments pink, 8–15 mm and 5–12 mm long; anthers oblong, 2.5–3 mm long, 1.5–2 mm wide, dull white. Style densely pilose in basal $\frac{1}{2}$ – $\frac{3}{4}$, pink; stigma globose, 4-lobed at apex, 2–3 mm long, 2–4 mm wide, cream to pink, exserted 5–15 mm beyond the anthers. Berry globose to ellipsoid, 8–18 mm long, 7–13 mm thick, dark red at maturity; seeds tan, 2–3 mm long, 1–1.5 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia and Venezuela. Low shrubs or lianas in thickets of high elevation cloud forest or in páramo shrub islands; in the Cordillera Oriental from Huila to Norte de Santander and just into Venezuela in southern Táchira; in the Cordillera Central from northern Valle to Antioquia; and in the Cordillera Occidental in Antioquia; (2,400–)2,900–3,900 m (Fig. 59).

Representative specimens examined: VENEZUELA, TÁCHIRA: between Fátima and San Vicente de la Revancha, *Fernández 1981* (MY); headwaters of the Río Quinimarí, above "Las Copas" below the Páramo de Judio, 18–20 km S of San Vicente de la Revancha, *Steyermark et al. 100795* (VEN). COLOMBIA, ANTIOQUIA: Páramo Frontino, near Llano Grande, *Boeke 250* (MO); summit of Morro Pelado, Anocosa-Abriaquí road, *Core 456* (RSA, US); Páramo de Sonsón, *Guarín 3470* (COL, US). BOYACÁ: Quebrada de San Paulino, near Alto Ritacuva, Sierra Nevada del Cocuy, *Barclay & Juajibioy 7279* (RSA); Páramos NW of Belén, headwaters of Quebrada Minas, *Cleef 1854* (U); between Soatá and Cocuy, Valle de la Uvita, El Hatico, *Cuatrecasas & García-Barriga 1161* (COL, F, US); between Soatá and Cocuy, Páramo del alto de Cañultal, *Cuatrecasas & García-Barriga 1183* (COL, F, US); Quebrada de Susacón, *Cuatrecasas & García-Barriga 9815* (COL, POM, US); above Guicán, Sierra Nevada de Cocuy, *Grubb et al. 70* (COL, K, MSC, US); near Laguna Seca, Sierra Nevada de Cocuy, *Grubb et al. 602* (COL, K, MSC, US); Ramiriquí, towards Laguna Negra, *Huertas & Camargo 6324* (COL); near Montalbán, road Duitama-Charalá, *Langenheim 3470* (COL, UC, US); Laguna la Colorada, Páramo de Pisba, *Rangel et al. 525* (COL); La Rusia, NW of Duitama, *Uribe-Uribe 1075* (COL, US). CALDAS: Páramo de Las Letras, *Barclay & Juajibioy 6293* (COL, MO, RSA); SW slopes of Nevado de Ruiz, Termales, *Cuatrecasas 9218* (COL, F, US); Páramo de Ruiz, *Lehmann 3067* (BM, K, US); 35 km NE of Manizales, *Madison 1335* (GH); San Félix, *Tomás 1866* (BH). CUNDINAMARCA: Subchoque to Cerro El Tablazo, *Berry 3539* (COL, MO); below Páramo de Choachí, *Berry 3542* (COL, MO); ridge between Fómeque and Laguna de Chingaza, Cuatro Vientos, *Cuatrecasas & Idrobo 26973* (US); Páramo de Chingaza, around Laguna Grande, *Cuatrecasas & Idrobo 26992* (US); Río San Juan, above San Juan, *Fosberg 20797* (RSA, US); Páramo de Sumapaz, Río Arroz, *Fosberg 20835* (US); near Bogotá, *Hartweg 990* (BM 2 sheets, BREM, CGE, K, OXF); Guadalupe, Bogotá, *Haught 5061* (POM, US), *5621* (COL, POM, US); Monserrate, Río de San Francisco, near Bogotá, *Hawkes & García-Barriga 69* (BM, COL, K, RSA, US); Páramo de Cruz Verde, near Bogotá, *Pennell 2056* (NY); Río San Cristobal, near Bogotá, *Pennell 2379* (GH, MO, NY, US); Boquerón de Chipaque, *Schneider 621a* (COL); Montserrate, *Triana 198* (K, P, US); La Calera, Páramo de Palacio, *Uribe-Uribe 6886* (COL); 20 km SE of Gigante, *Little 8686* (US). META: Río Arroz, well above confluence of Quebrada Pedregal, *Fosberg 20916* (US). NORTE DE SANTANDER: 7 km above Pamplona to Bucaramanga, *Berry 3533* (MO); Chitagá, near Presidente, *Cuatrecasas & García-Barriga 10053* (COL, F); Pamplona, *Funck & Schlim 1646* (BM, CGE, F, G, LE, OXF, P, W); 20 km S of Abrego, Las Jurisdicciones, Cerro de Oroque, border with Dept. Cesar, *García-Barriga & Jaramillo 19758* (COL), *19808* (COL); around Ocaña, *Kalbreyer 426* (K); between Mutiscua and Pamplona, *Killip & Smith 19734* (A, GH, NY, US); W slopes Páramo del Hatico, Toledo to Pamplona, *Killip & Smith 20714* (GH, NY, US); Pica-pica valley, above Tapatá, N of Toledo, *Killip & Smith 21121* (GH, NY). QUINDÍO: Alaska, above Salento, *Pennell 9381* (PH); Páramo del Quindío, *Pennell & Hazen 10058* (NY, PH). RISARALDA: Campoalegre-San Ramón ridge, E of Santa Rosa de Cabal, *St. John 20850* (COL, NY, RSA, US). SANTANDER: Páramo de la Cruces, *Funck & Schlim 1307* (BM, G, LE, P, W); La Baja, *Funck & Schlim 1305* (BM, G 2 sheets, LE, OXF, W); edge of Páramo Las Vegas, *Killip & Smith 15734* (A, F, NY, US); between California and Las Vegas, *Killip & Smith 17236* (A, GH, NY, US); vicinity of Vetás, *Killip & Smith 17335* (A, GH, US), *17361* (A, GH, NY, US), *17386* (A, GH, NY, US); W slopes of Páramo Rico, *Killip & Smith 17755* (A, F, GH, NY, US), *17771* (A, GH, NY, US); Páramo de las Puenteas, above La Baja, *Killip & Smith 18211* (A, GH, NY, US); Páramo de Romeral, *Killip & Smith 18577* (A, GH, NY, US). TOLIMA: 47–48 km W of Fresno to Manizales, *Berry 3558* (COL, MO), *3559* (COL, MO); SE slopes Mt. Tolima, Las Mesetas, *Cuatrecasas 2615* (MA 2 sheets); Quindío-La Linea, *Dryander 1939* (US); Volcancitos, *Holton 896* (G, GH, K, NY, UC); along divide near Quindío highway, *Killip & Varela 34600* (BM, COL, POM, US); Quindío, *Humboldt & Bonpland s.n.* (P); Rosalito, near Páramo de Ruiz, *Pennell 3121* (F, GH, MO, NY, US). VALLE: Páramo de Bavaya, Barragán, drainage of Río Bugalagrande, *Cuatrecasas 20042* (F, US, VALLE); Quebrada de Las Vegas páramo, headwaters of Río Tuluá, *Cuatrecasas 20249* (F, VALLE).

This is one of the polymorphic, long-tubed, axillary-flowered species of the *Fuchsia petiolaris* species group that are found at high altitudes in the northern Andes. Its main distinguishing characteristics are the slightly constricted floral tubes at the rim (in most cases), the typically ovate-lanceolate sepals that flare out conspicuously at the base from the rim of the floral tube, and the acute, elliptic to lanceolate petals that are usually puberulent or villous on the dorsal surface. The petals are always smaller than the sepals and in some populations are less than half as long. Its closest relative is probably *F. corollata*, which occurs south of the range of *F. petiolaris* in the Cordillera Central. A list of their

TABLE 10. Distinguishing characters of *Fuchsia petiolaris* and *F. corollata*.

	<i>F. petiolaris</i>	<i>F. corollata</i>
Leaf texture (when dry)	Smooth	Slightly bullate
Leaf surface (when dry)	Matte	Glossy
Length of glandular teeth on margin	0.1–0.3 mm	0.3–0.5 mm
Floral tube constricted at rim	Usually	No
Floral tube pubescence	Puberulent	Strigose
Petal shape	Lanceolate-elliptic	Rhombic-broadly elliptic
Petal apex	Acute	Obtuse to cuneate
Petal pubescence (dorsal side)	Puberulent to villous, rarely glabrous	Glabrous
Style pubescence	Densely pilose in basal 1/2–3/4	Glabrous to occasionally pi- lose

distinguishing characters is given in Table 10. The possible affinities of *F. petiolaris* outside of its species group are with *F. gehrigeri*, which commonly has pubescent petals, and similarly large seeds and globose fruits.

Characters that vary widely in *F. petiolaris* are leaf size and shape, floral dimensions, pubescence type on stems and petals, and the size and shape of the berries. Most of the size differences can be attributed to ecological factors. Short petiolate, small-leaved and short-flowered plants typically are found in high, exposed habitats or in trees near open páramo. Well shaded plants in lower, more protected sites are usually more robust, with longer pedicels, and larger leaves and flowers.

Geographical patterns of variation exist in characters such as pubescence and leaf shape, but individuals typical of one area can always be found in the other areas as well. In view of this wide degree of local and regional polymorphism, any attempt to subdivide this group taxonomically seems unwarranted. Some of the patterns of variation are described in the following paragraphs.

Most collections from the northern part of the Cordillera Oriental of Colombia (Boyacá to Norte de Santander) and just over the border into Táchira, Venezuela have short pilose, ferrugineous stem pubescence. Such plants were treated by Munz as *Fuchsia smithii*, and these also differ from most populations from Cundinamarca and the Cordillera Central in their larger, narrower, more reticulate-veined leaves, petals villous mostly along the midvein, and larger, more cylindrical fruits. Variation within this area can also be considerable, however. *Grubb et al.* 602 (COL, K, US) has floral tubes 52 mm long but only 5 mm wide; *Cuatrecasas & García-Barriga* 10053 (COL, F) has the largest flowers in the species, with tubes 62 mm long and 11 mm wide. Its leaves are broad and nearly entire, unlike most collections from this area.

Some plants of the type described above reach south to Cundinamarca, such as *Cuatrecasas & Idrobo* 26973 (US). Plants from the Bogotá area are especially variable, however, but for the most part have fine, canescent vegetative pubescence and round fruits. The degree of petal pubescence is exceedingly variable between populations around Bogotá, with some puberulent over the entire adaxial surface, as in *Hawkes & García-Barriga* 69 (BM, COL, K, RSA, US), and others that are entirely glabrous, as in *Haught* 5621 (COL, POM, US). The type spec-

imens of *F. petiolaris* and *F. curviflora* are both from the vicinity of Bogotá. The slight curvature of the tubes in *F. curviflora* is not unusual, and though the sepals of the dried specimen are pale, they are by no means white as the description states.

Fuchsia petiolaris is widespread in the Nevado de Ruiz Massif of the Cordillera Central, following the same distribution pattern as *F. venusta*, *F. hirtella*, and *F. nigricans*, all of which are present in both the Cordillera Oriental and the Cordillera Central. Many individuals with small leaves and flowers are found in this area; these plants are often found in trees or in exposed páramo shrub islands where stunting is a common response to the harsh climatic conditions. *Fuchsia quinduensis* was apparently described from one such stunted plant, and *Sandeman 5672* (K, OXF) is a particularly good example of leaf reduction in an exposed plant. Sometimes large, petiolate leaves can be found on the basal portions of specimens that have nearly sessile, tightly grouped small leaves on the upper branches. Sepals on plants from the Cordillera Central are usually more flared at the base than ones from the Cordillera Oriental, and they sometimes split open in bud in the middle before the tips become separated. Petals are puberulent over the entire surface and are mostly narrowly lanceolate and much smaller than the sepals. The fruits are generally small and globose as in most Cundinamarca collections, but the flowers are usually puberulent, and the stems are sometimes ferrugineous as in many Santander collections.

Fuchsia petiolaris has also reached the high northern peaks of the Cordillera Occidental in Antioquia. Although *Boeke 256* (MO), from Páramo Frontino, has long, slender flowers (51–55 mm long, 6–8 mm wide), other characters such as petal shape and pubescence are well within the range of *F. petiolaris*.

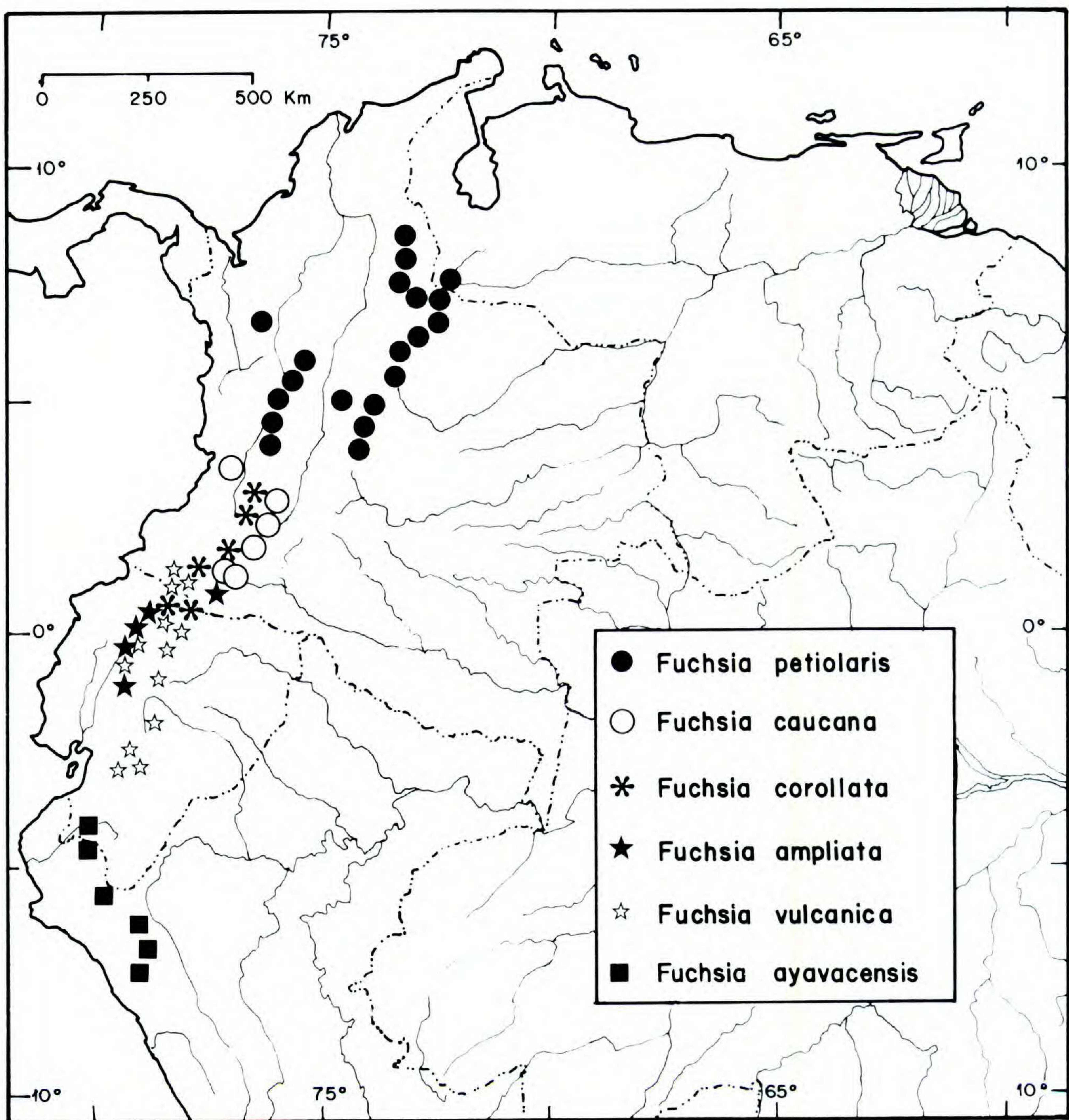
Since *Fuchsia petiolaris* is the highest altitude species in its range, it usually occurs alone, but in the Cordillera Central it is occasionally sympatric with *F. hirtella* and *F. hartwegii*. It would be of considerable interest to examine more populations of the Cordillera Central between Valle and Cauca, to see if transitional populations occur between the closely related *F. petiolaris* and *F. corollata*.

23. ***Fuchsia corollata*** Benth. Pl. Hartw. 179. 1845. TYPE: Colombia, Dept. Cauca, near Popayán in woods of Puracé, ascent to Páramo de Guanacas, ca. 3,000 m, 1842, *Theodor Hartweg 993* (K Benth. Herb., holotype; photograph, MO; BM, BREM, CGE 2 sheets, F, G, K Hooker Herb., LE, OXF, P, W 2 sheets, isotypes).

Fuchsia canescens sensu Munz, Proc. Calif. Acad. Sci. IV. 25:26. 1943; Opera Bot., Ser. B, 3:12. 1974.

Fuchsia colombiana Munz, Caldasia 4:109, 110, fig. 1946. TYPE: Colombia, Dept. Cauca, Cordillera Central, W slopes, headwaters of Río Palo, páramos between la Quebrada del Duende and Las Casitas, 3,500–3,600 m, 3 Dec. 1944, *José Cuatrecasas 18959* (A, holotype; COL, isotype).

Erect to scandent shrubs 0.5–5 m tall with ascending to divergent branches. Branchlets terete, 2–3 mm thick, strigose, generally red purple; older stems 5–12 mm thick with red tan, exfoliating bark. Leaves ternate or less often quaternate, firmly membranous to subcoriaceous, elliptic to oblanceolate, acute to narrowly cuneate at the base, acute to obtuse at the apex, 20–70 mm long, 7–30 mm

FIGURE 59. Distribution of the *Fuchsia petiolaris* species group.

wide, dark glossy green and glabrous to strigose above, pale green and usually strigose or villous below; secondary veins 3–8 on either side of the midvein, often red below; margin gland-serrulate, the teeth usually conspicuous and mostly 0.3–0.5 mm long. Petioles strigose, 3–12(–22) mm long. Stipules lance-linear, dark, 2–4 mm long, 0.7–1 mm wide, persistent and usually divergent. Flowers axillary and pendant, usually fewer than 6 per branch. Pedicels 12–24 mm long. Ovary ovoid-ellipsoid, 6–7 mm long, 2–2.5 mm thick, subglabrous to strigose. Floral tubes narrowly funnelform, (28–)35–55(–60) mm long, 2.5–3 mm wide and bulbous at base, then narrowed to 1.5–2 mm and gradually widened above until 5–8 mm wide at rim, subglabrous to strigose outside, villous inside in lower ½. Sepals lanceolate to ovate-lanceolate, subacuminate at apex, 10–17(–22) mm long, 5–6(–8) mm wide, sometimes split open in middle in bud, spreading to divergent at an-

thesis. Tube subnitid red pink to scarlet; sepals paler, often greenish towards tips. Petals scarlet, almost always longer than sepals, (broadly) elliptic to rhombic, obtuse to cuneate at apex, attenuate to unguiculate at base, 10–18(–24) mm long, (5–)6–10 mm wide, glabrous to rarely pilose on dorsal nerve, (strongly) spreading at anthesis. Nectary unlobed or shallowly 4-lobed, 1.5–2 mm high, sometimes with a few erect hairs. Filaments red pink, 10–18 mm and 7–15 mm long; anthers oblong to subreniform, 2–3 mm long, 1.5–2.2 mm wide, cream. Style red, glabrous or occasionally pilose; stigma globose, slightly 4-cleft at apex, 2–3 mm long, 2–4 mm wide, cream to light red. Berry subglobose, 9–13 mm long, 8–10 mm thick, purple at maturity; seeds tan, 2–2.6(–3) mm long, (1.0–)1.2–1.6(–2) mm wide. Gametic chromosome number $n = 11, 22$.

Distribution: Southern Colombia and northern Ecuador; high elevation cloud forest and subpáramo shrubs from the Cordillera Central of Colombia in Cauca south to Imbabura, Ecuador, 2,800–3,800 m (Fig. 59).

Representative specimens: COLOMBIA, CAUCA: Pilimbalá, N slopes Volcán Puracé, *Aguirre 311* (COL); 11 km E of Totoró to Inzá, *Berry 3575* (COL, MO); 4 km W of Gabriel López, road Totoró-Inzá, *Berry 3576* (COL, MO); 17 km E of Puracé, *Berry 3582* (MO); headwaters of Río Palo, Quebrada del Duende, *Cuatrecasas 18931* (BH, F, GH, VALLE); Finca Las Mercedes, near Silvia, *Granger & Rodríguez 17* (RSA, US); Manchai, NE of Silvia, *Haught 5122* (COL, POM, US); Páramo Las Delicias, *Lehmann B.T.1058* (GH, K, NY); Paletará, *Pennell 7004* (GH, PH); Páramo de Buena Vista, Huila group, *Pittier 1188* (US). NARIÑO: between Pasto and Túquerres, *André 3182* (K); “El Páramo,” Km 15 of Pasto-Ipiales road, *Berry 3146* (MO); Páramo El Támano, road Pasto-Laguna La Cocha, *Berry 3249* (MO, PSO); 18 km above Pasto, road to Tangua, *Ewan 15918* (BM, DS, POM, US); Laguna La Cocha, *Ewan 16381* (POM, US); road Túquerres-Ipiales, *García-Barriga & Hawkes 13073* (COL, US); road Ipiales-La Victoria, Páramo de la Cortadera, *García-Barriga & Hawkes 13091A* (COL); Volcán de Sotará, *Lehmann 6196* (K); trail from Sapuyes to Páramo de Gualaratán, *Mora 2901* (PSO); Pasto, base of Volcán Galeras, above Obonuco, *Schultes & Villarreal 8023* (COL, RSA, US); Tangua, Cubiján trail, *Uribe-Uribe 5302* (COL, PSO, US). ECUADOR, CARCHI: Tulcán-El Carmelo road, 7 km E of Panamerican Highway, *Berry 3158* (MO), *3159* (MO); between El Carmelo and Santa Bárbara, *Berry 3165* (MO); road Tulcán-El Pun (= El Carmelo), *Mexia 7584* (BH, K, RSA, UC, US). IMBABURA: Hacienda Curubí, 10 km W of Otavalo towards Mojanda, *Berry 3173* (MO, QCA); 11 km W of Otavalo to Laguna de Mojanda, *Berry 3175* (MO, QCA); Mojanda, ca. 10 km SSW of Otavalo, *Sparre 13523* (S).

Probable hybrids between *Fuchsia corollata* and *F. caucana*: COLOMBIA, CAUCA: Páramo de Las Papas, near Laguna Cusiyaco, *Barclay & Juajibioy 5936* (COL, RSA); Volcán de Puracé, *Barkley et al. 18ca.112* (US); 45 km from Popayán on road to Volcán Puracé, *Barkley & Mullen 38C712* (COL, GH); 23–35 km E of Puracé, road to La Plata, *Berry 3583* (COL), *3584* (MO), *3585* (COL, MO); Páramo de Puracé, S of Volcán Puracé along divide, San Francisco, *Cuatrecasas 14644* (BH, F, VALLE); Páramo de Juntas, Km 53 (extension of Páramo de Guanacas), *Cuatrecasas & Willard 26375* (COL); W side of Páramo de Puracé, *Killip & Lehmann 38602* (BH, US); Páramo de Las Papas, between El Boquerón and La Hoyola, *Idrobo et al. 3935* (COL); road Popayán to Puracé, Parque Nacional Puracé, *Lozano & Ruiz 1518* (COL); Parque Nacional Puracé, *Plowman et al. 5335* (COL), *von Sneider 1843* (S), *1847* (S), *1848* (S), *Uribe-Uribe 3845* (COL, MO). HUILA: 35–40 km E of Puracé on road to La Plata, *Berry 3586* (COL, MO), *3588* (COL, MO).

This is one of several closely allied and polymorphic species in the *Fuchsia petiolaris* species group from high elevations in the Colombian and Ecuadorian Andes. Its most characteristic features are the elliptic-rhombic petals usually exceeding the size of the sepals and the glossy, firm, gland-denticulate leaves that often dry with a slightly bullate texture. Its closest relative is *F. petiolaris*, which occurs in the Cordillera Oriental and Cordillera Central just north of the range of *F. corollata*. Since these species are widespread and variable, clear recognition of the species limits between them can be difficult, especially if one is dealing

only with herbarium specimens. Furthermore, we do not yet know if the two species intergrade in southern Valle Dept. or northern Cauca, where their ranges are in close proximity. Based on the existing specimens, Table 10 presents a summary of characters that can be used to distinguish *F. corollata* from *F. petiolaris*. It must be noted, however, that hybrids of *F. corollata* with other fuchsias are apparently widespread in southern Colombia, and these individuals would generally fall outside the limits designated for the above species.

Munz (1943, 1974) mistakenly synonymized this species under *Fuchsia canescens* because of an erroneously numbered Hartweg collection from Geneva that he examined. *Hartweg 992* is the type number of *F. canescens*, but the specimen at G does not correspond to the holotype at K. It is rather a duplicate of *Hartweg 993*, the type collection of *F. corollata*. Munz was not able to examine the holotypes or other isotypes of these species, so he concluded that *F. corollata* was a synonym of *F. canescens*. The latter species is now known with certainty to be distinct and much rarer than *F. corollata*; it is found mostly on the eastern slopes of the Cordillera Central in southern Colombia and has thick-tubed, orange, canescent flowers and larger leaves than *F. corollata*.

Morphologically similar populations of *F. corollata* are found from Cauca, Colombia to Imbabura, Ecuador. The species may even reach as far south as Pichincha, but the single collection there, *Benoist 4547* (P; west side of Volcán Pichincha), has rather narrow flowers and pilose styles for this species. Different ploidy levels have been found in different parts of the range of *F. corollata*, however. Two collections from nearby populations in Cauca were diploid, and three counts from two distinct populations in Ecuador were tetraploid (Table 4). The only differences noted between these groups were that the tetraploid populations had slightly larger seeds, more markedly rhombic petals with a narrow base, and a common pyramidal shaped growth habit, with sharply ascending branchlets. Their pollen also has variable proportions of triporate grains. Most of these morphological characters vary within the tetraploid populations, however, and some of the Imbabura individuals even have petals that are shorter than the sepals.

Two collections from the western slopes of the Cordillera Occidental in Carchi, Ecuador, *Holm-Nielsen et al. 5580* (AAU, S) and *5674* (S; both from Km 53 of Tulcán-Maldonado road, 3,150–3,250 m), have certain characters of *F. corollata* such as somewhat rhombic petals and green sepal tips in bud, but they have nearly entire, quaternate, membranous leaves that are not typical of this species. More cytological examination and population sampling from southern Colombia (Cauca and Nariño) would help to establish the pattern of ploidy level in *F. corollata* and to detect if any further morphological differences can be correlated with either diploid or tetraploid populations.

A substantial number of specimens from Cauca differ from typical *F. corollata* populations in one or more of the following characters: small, lanceolate leaves 15–30 mm long, few (2–4) secondary veins, entire or subentire leaf margins, petals shorter than the sepals, long floral tubes mostly 55–70 mm long, and the presence of triporate pollen grains. These collections, which are listed separately at the end of the specimens citation list, are believed to be hybrids between *F. corollata* and *F. caucana*. A series of these probable hybrids was examined in

June 1979 along the road from Popayán to La Plata, in Cauca and Huila Depts., on the north face of Volcán Puracé. Ascending from Popayán from the west, *F. corollata* (Berry 3582; COL, MO) was collected with *F. canescens* at 3,235 m. Berry 3583 to 3586 (COL, MO) were collected farther east, at higher elevations in semi-open subpáramo habitats near the divide of the Cordillera Central. Each number of this series comes from a different population along a stretch of several km, where extreme variability in leaf shape and floral dimensions was found. Starting to descend to the east, the first plant recognized as *F. caucana* (Berry 3587; COL, MO) was found at ca. 3,100 m growing next to one of the variable forms typical of the upper, intermediate area (Berry 3588; COL, MO). Between 10% and 20% of the pollen in the suspected hybrids, Berry 3583, 3584, 3586, and 3588, have triporate grains, and stainability varies from 20% in Berry 3583 to 80% in Berry 3584. Triporate grains in *Fuchsia* are sometimes indicators of polyploidy, and gametic and somatic counts of Berry 3584 indeed proved to be tetraploid. The two counts of *F. corollata* from Cauca and the one count of *F. caucana* from Nariño are all diploid, however, and both Berry 3582 (*F. corollata*) and Berry 3588 (*F. caucana*) have entirely biporate and highly stainable (>95%) pollen grains. It is possible, then, that if all the variable collections along the exposed ridge of the Páramo de Puracé are tetraploids, they originated as allotetraploid hybrids of *F. corollata* and *F. caucana*. This is only hypothetical, but could be analyzed experimentally. Additional evidence of hybrid origin for the above series is available from Berry 3584. Normal pairing of 22 bivalents was found in meiotic preparations, but the only ripe fruit found on the plant had 35 aborted seeds and 13 ripe ones. These seeds were germinated along with other collections at the University of California Botanical Gardens at Berkeley in 1980, but only one small, weak seedling developed, from which the tetraploid root tip count was made.

Another area where collections variable in leaf texture and petal size occur is the Páramo de Las Papas area of the Macizo Colombiano in southern Cauca. Hybridization may be the cause of this variability as well. The type of *F. colombiana*, Cuatrecasas 18959 (A), from northern Cauca, is distinguished by its extremely reduced leaves less than 2 cm long, but this may be due at least in part to the high elevation (3,500–3,600 m) where it was collected. Its leaves are not very different from individuals such as Berry 3585, from the probable hybrid series discussed above.

Fuchsia corollata is found in close proximity to *F. caucana* in Nariño, and it occurs sympatrically with *F. canescens*, *F. dependens*, and *F. sessilifolia*.

24. *Fuchsia caucana* P. Berry, sp. nov. TYPE: Colombia, Dept. Cauca, 31 km E of Totoró on road to Inzá, E slopes of Cordillera Central, 3,240 m, 8 June 1979, Paul E. Berry 3577 (COL 107163, holotype; MO 2 sheets, isotypes). Fig. 26.

Fuchsia petiolaris sensu Munz, Proc. Calif. Acad. Sci. IV. 25:34. 1943, pro parte.

Frutex (0.3–)0.5–2 m altus plerumque pauciramosus. Ramuli teretes, subglabrati vel strigosi vel puberuli, albo-virides vel rubro-purpurei; caulibus glabrescentibus cortice subnitida purpureo-brunnea. Folia plerumque ternata interdum opposita raro quaterna, firme membranacea, (anguste) elliptica vel lanceolato-ovata, basi acuta vel rotundata, apice plerumque acuminata, (2.5–)3.5–7(–10) cm longa, (1–)1.5–3.2(–4) cm lata, supra obscure atroviridia, subglabrata sparsim vel strigulosa, subtus pallide

albo-viridia vel strigosa nervis secundariis utroque latere (3–)5–6(–7) subtus saepe rubris, paralleli-nervis; margine conspicue glanduloso-serrulata, raro subintegerrima; petiolis saepe rubro-purpureis, 2–13(–14) mm longis; stipulis anguste lanceolatis vel linearibus, fuscatis, 3–4 mm longis, 0.5–1 mm latis, subpersistentibus. Flores roseo-cerasinii vel (pallide) purpureo-lavandulacei, pauci in axillis supernis ramorum dispositi; pedicellis dependentibus, 12–28 mm longis; ovario ovoideo-ellipsoideo, glabro vel puberulenti-strigoso, 5–6 mm longo. Tubi florales anguste infundibuliformes, 32–45(–54) mm longi, basi 2–4 mm lati parum bulbosi, plerumque constricti $\frac{1}{3}$ parte inferiore inde saepe $\pm$ abrupte dilatati, summo 4–11 mm lati, extus glabrati vel puberulenti, intus pilosi. Sepala lanceolata (sub)acu-minata (12–)14–17(–22) mm longa, 5–6 mm lata, alabastro apice interdum albido-viridi. Petala plerumque valde breviora quam sepalis, atrorubra vel purpurea, elliptico-ovata, 9–11(–14) mm longa, 5–6(–9) mm lata, obtusa vel cuneata apice interdum mucronulata. Filamenta rosea, antisepala 8–10 mm longa, antipetala 5–7 mm longa; antheris oblongis 3–4 mm longis, 2–3 mm latis luteo-eburneis. Stylus usque ad summum tubi floralis dense pilosus, roseo-ruber; stigmatibus roseo, late capitato, tetra-gono, 2–3 mm long, 3.5–4 mm lato, apice leviter 4-fisso. Bacca ante maturitatem 4-sulcata, glabrata vel puberulento-strigosa, in maturitate subglobosa, 11–13 mm longa, 7–9 mm crassa, nitida rubro-purpurea; seminibus rubro-brunneis vel vivide rubris, 2–2.5 mm longis, 1.1–1.8 mm latis. Numerus gameticus chromosomatum $n = 11$.

Usually few-branched shrubs (0.3–)0.5–2 m tall. Branchlets terete, 2–5 mm thick, subglabrous to strigose or puberulent, white green to red purple; older stems with subnitid, purple brown bark. Leaves mostly ternate, occasionally opposite or quaternate, firmly membranous, (narrowly) elliptic to lance-ovate, acute to rounded at the base, mostly acuminate at the apex, (2.5–)3.5–7(–10) cm long, (1–)1.5–3.2(–4) cm wide, dark velvety green and subglabrous to sparsely strigose above, pale whitish green to deep flushed purple and strigose below; secondary veins (3–)5–6(–7) on either side of the midvein, subparallel and as-cending towards the tip at ca. 45° to the midvein; margins serrulate with con-spicuous glandular teeth, rarely subentire. Petioles glabrous to strigose, usually red purple, 2–13(–14) mm long. Stipules narrowly lanceolate to linear, 3–4 mm long, 0.5–1 mm wide, subpersistent. Flowers few in upper leaf axils. Pedicels pendant, 12–28 mm long. Ovary ovoid-ellipsoid, glabrous to puberulent or stri-gose, 5–6 mm long, 2.5–3 mm thick. Floral tube narrowly funnelform, occasion-ally dilated in the middle and constricted again near the rim, 32–45(–54) mm long, 2–4 mm wide and slightly bulbous at the base, usually narrowed to 1.5–3 mm in lower $\frac{1}{3}$, then widened to 4–11 mm wide at the rim, glabrous to strigose or puberulent outside, pilose inside for most or the entire length. Sepals lanceolate, (sub-)acuminate at the apex, (12–)14–17(–22) mm long, 5–6 mm wide, with a short point 1–2 mm long in bud, spreading at anthesis. Tube and sepals pink cerise to (light) purple lavender, young buds sometimes whitish green. Petals usually con-siderably darker than the sepals, (dark) red-purple, elliptic-ovate, 9–11(–14) mm long, 5–6(–9) mm wide, obtuse to cuneate or sometimes mucronate at the apex, suberect at anthesis. Nectary unlobed, ca. 2 mm high. Filaments pink, 8–10 mm and 5–7 mm long; anthers oblong, 3–4 mm long, 2–3 mm wide, yellow cream. Style densely pilose from base to near the rim, red pink; stigma broadly capitate, tetragonous, slightly 4-cleft apically, 2–3 mm long, 3–4 mm wide, pink, exerted 7–16 mm beyond the anthers. Berry 4-sulcate before maturity, glabrous to strigose or puberulent, subglobose at maturity, 11–13 mm long, 7–9 mm thick, lustrous red purple; seeds reddish brown to bright red, 2–2.5 mm long, 1.1–1.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Colombia. Low shrubs in open thickets in high ele-vation elfin cloud forest, eastern slopes of the Cordillera Central in Cauca, Huila,

Nariño, and Putumayo, and in the Cordillera Occidental in the Farallones de Cali, Valle, 2,700–3,600 m (Fig. 59).

Representative specimens examined: COLOMBIA, CAUCA: near Río Grande, between San Andrés and Alto Todos los Santos, *Core* 1060 (RSA); between Jardín and San Rafael, Quebrada del Río San Marcos, *Cuatrecasas* 14711 (F); Alto del Buey, *Escobar & Escobar* 1143 (MO); Páramo de Guanacas, *Lehmann* 5616 (K); Parque Nacional Puracé, Paletará, *Luteyn & Lebrón-Luteyn* 6948 (NY); Puracé, Moscopán, *Yepes-Agreto* 274 (COL). HUILA: between Leticia and Parque Nacional Puracé, 63 km SW of La Plata, *Aguirre* 274 (COL); 37–40 km E of Puracé, road to La Plata, *Berry* 3587 (COL, MO), 3590 (COL, MO). NARIÑO: Páramo de Quilinsayaco, between El Encano and Santiago, *Barclay & Juajibioy* 9470 (RSA); above El Encano, Laguna La Cocha, *Balls* B7504 (BM, K, NA, UC, US); 24 km E of Pasto on road to Mocoa, *Berry* 3252 (MO, PSO); Páramo de Bordoncillo, *Espinal* 1023 (COL, PSO); 34 km E of Pasto, Páramo de Quilinsayaco, *Espinosa* E3089 (NY); above Laguna La Cocha, 16 km ESE of Pasto, *Fosberg* 20445 (RSA, US); El Tábano, *García-Barriga* 4560 (COL, US); Buesaco, *García-Barriga et al.* 13016 (COL, US); Laguna La Cocha, Ciudadela, near Páramo de Bordoncillo, *Schultes & Villarreal* 7575 (COL, GH, K, NY, RSA, US). PUTUMAYO: between Santiago and Laguna La Cocha, *Alston* 8398 (BM, COL, K, RSA); 8 km N of Sibundoy, *Bristol* 823 (DS, PSO); La Cabaña, headwaters of Río Sibundoy, valley of Sibundoy, *Cuatrecasas* 11598 (COL, F, US); Páramo de Bordoncillo, *Cuatrecasas* 11709 (COL, US); Páramo El Capuchino, between El Encano and Sibundoy, *García-Barriga et al.* 18581 (COL); Páramo de San Antonio, between Laguna La Cocha and Sibundoy, *Schultes* 3225 (DS, GH, NY); between La María and Páramo de San Antonio, road from Sibundoy to Pasto, *Schultes & Villarreal* 7827 (GH, RSA).

Fuchsia caucana is allied to other long-tubed, axillary-flowered, high-elevation species such as *F. corollata* and *F. petiolaris*. Munz included the specimens he saw of this species under *F. petiolaris*, but *F. caucana* is clearly distinct from that species both morphologically and geographically. Part of this confusion is due to the loss of key characters upon drying, making it difficult to distinguish this species when just herbarium specimens are available. *Fuchsia caucana* can generally be distinguished, though, by its acuminate-tipped leaves with few secondary veins that ascend toward the tip at a sharp ($\pm 45^\circ$) angle from the midvein. When fresh, the leaves are mostly a matte, velvety green above and much paler or often purple-flushed below. This contrasts with the glossy, dark foliage of *F. corollata*. The floral tubes are different shades of lavender or pink purple, unlike the redder flowers of *F. petiolaris* and *F. corollata*. The petals are often a deep purple and are always darker and considerably shorter than the sepals. In *F. corollata*, the petals usually exceed the sepals and are scarlet colored.

Some variation in tube shape and pubescence occurs between different populations. In Huila and Cauca, most plants are glabrous or strigose with floral tubes that are usually somewhat constricted at the rim. Plants from Nariño and Putumayo are commonly puberulent with narrowly funnelform tubes widest at the rim. The disjunct populations from the Cordillera Occidental in Valle are well within the variation present in the Cordillera Central.

Fuchsia caucana is sympatric with *F. canescens* on the upper, eastern slopes of the Cordillera Central in Cauca and Nariño. Probable hybrids are found around the type locality on the road from Totoró to Inzá and are discussed under *F. canescens*. Extensive intergradation between *F. caucana* and *F. corollata* occurs along the high ridge of the Cordillera Central on slopes of Volcán Puracé and in the Páramo de Las Papas area. *Fuchsia caucana* is only found on the eastern slopes, and *F. corollata* grows mostly on the western slopes; where they approach each other near the ridge of the cordillera, widely variable local populations are found with reduced leaves and floral tubes that are often longer than either of the

supposed parental species, but with intermediate petal size. These populations are discussed in greater detail under *F. corollata*.

- 25. *Fuchsia ayavacensis*** Humboldt, Bonpland & Kunth, Nov. Gen. Pl. 6:107. 1823. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):549. 1941, pro parte. Munz, Proc. Calif. Acad. Sci. IV. 25:21. 1943, pro parte; Opera Bot., Ser. B, 3:11. 1974, pro parte. TYPE: Peru, Dept. Piura, near Ayabaca, ca. 2,850 m, Aug. 1802, *Alexander von Humboldt & Aimé Bonpland* (P, holotype, not seen; photograph, F; microfiche, MO).

Fuchsia townsendii I. M. Johnston, Contr. Gray Herb. 75:33. 1925. TYPE: Ecuador, Prov. Loja, Sabiango Hill, 26 Nov. 1910, *Charles H. T. Townsend* A93 (US, holotype; photographs, NY, UC; fragment, GH).

Fuchsia asplundii J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):548. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:37, pl. 4, fig. 24. 1943. TYPE: Peru, Dept. Piura, Prov. Huancabamba, above Palambla, 3,000 m, April 1912, *August Weberbauer* 6054 (F, holotype; photographs, NY, POM, UC; G, GH, US, isotypes).

Suberect to scandent shrubs 1–4 m tall with flexuous branches to several m long when scandent. Young growth densely canescent-strigose or hirtellous with whitish hairs, older portions strigose to hirtellous; older branches with brown, exfoliating bark. Leaves mostly ternate, occasionally quaternate, membranous, oblong to elliptic or narrowly elliptic-oblong, acute at the base, acute to subacuminate at the apex, 6–15(–18) cm long, 2.2–5(–7) cm wide, matte green and strigillose above, paler and strigose below, sometimes red-tinged; secondary veins 7–12 on either side of the midvein, at times reddish below; margin subentire to denticulate. Petioles 6–20(–30) mm long. Stipules lanceolate to triangular, 1.5–2 mm long, mostly deciduous. Flowers axillary at branch tips. Pedicels 6–25(–50) mm long, drooping. Ovary ellipsoid, 6–8 mm long, 2–3 mm thick. Floral tube narrowly funnelform, (35–)40–55 mm long, 3–3.5 mm wide and bulbous at the base, narrowed to 2–2.5 mm wide above the nectary and gradually widened above until 5–8 mm wide at the rim, subtetragonous in transection, strigose outside, pilose inside in lower ½. Sepals lanceolate, acuminate, 10–20 mm long, 4–6 mm wide, spreading to divergent at anthesis. Tube and sepals orange red. Petals orange red, broadly elliptic-ovate, rounded to subacute at the apex, 7–11 long, 5.5–8 mm wide, mostly about half as long as the sepals. Nectary unlobed or shallowly 4-lobed, 1.5–2 mm high. Filaments light red, 8–11 mm and 5–8 mm long; anthers oblong, 2.5–3 mm long, ca. 2 mm wide, white. Style light red, pilose in lower ½; stigma subobconic, 4-cleft apically, ca. 3 mm long, 3–4 mm wide, light red. Berry ellipsoid, 16–20 mm long, 8–10 mm thick, strigose, reddish; seeds 1.3–1.6 mm long, 0.8–1.1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Depts. Cajamarca and Piura of northern Peru and southernmost Loja Prov. of southern Ecuador; scattered to locally frequent shrubs in secondary woods, cut-over slopes, and in thickets of moist montane forest; 1,900–3,200 m (Fig. 59).

Representative specimens examined: PERU, CAJAMARCA: between Cascas and Contumazá, *Berry & Escobar* 3601 (MO, USM); Hacienda Taulis, between the Casa Hacienda and Palmito, Prov. Hualgayoc, *Hutchison & Bismark* 6401 (F, G, LE, MICH, MO, NY, RSA, UC, US, USM); Socotá to San Andrés, *López & Sagástegui* 5372 (MO); Prov. San Miguel, *Weberbauer* 3903 (G). PIURA: 5 km

above Canchaque on road to Huancabamba, *Berry & Escobar* 3630 (MO, USM); 38 km above Canchaque to Huancabamba, just below summit of road, *Hutchison & Wright* 6577 (RSA, UC, USM); Bajada de Ayabaca to El Puente, *Ochoa* 1782 (DS); Ciénaga Larga, Huancabamba to Cuello del Indio, *Sagástegui et al.* 8526 (MO); Ayabaca, *Soukup* 4349 (US).

This is the southernmost member of the *Fuchsia petiolaris* species group. Munz (1943, 1974) confused it with *F. ampliata*, which occurs in central Ecuador and has much larger, rounder petals, wider floral tubes, and strongly reflexed sepals. *Fuchsia vulcanica* can also be confused with this species, but it generally has smaller leaves with shorter petioles and larger, wider petals. *Fuchsia ayavacensis* is characterized by its large, dull leaves with whitish, strigose-hirtellous pubescence and its often scrambling habit with long, flexuous branches. It has not been found to occur sympatrically with any other species in the section, and it is the only species centered in the relatively dry Cordillera Occidental of Peru. It grows there in moist scrub thickets and in the southernmost remnants of cloud forest on the west side of the Andes.

- 26. *Fuchsia vulcanica*** André, Rev. Hort. 60:233, 268. 1888. TYPE: Colombia, Dept. Nariño, Volcán Azufral, near Túquerres, 18 May 1876, *Édouard André* 3228 (K, holotype; photograph, MO).

Fuchsia hitchcockii I. M. Johnston, Contr. Gray Herb. 75:33. 1925. TYPE: Ecuador, Prov. Azuay, between Oña and Cuenca, 2,700–3,300 m, 9–10 Sept. 1923, *Albert S. Hitchcock* 21603 (GH, holotype; NY, US, isotypes).

Fuchsia ayavacensis sensu Munz, Proc. Calif. Acad. Sci. IV. 25:32. 1943, pro parte; Opera Bot., Ser. B, 3:11. 1974, pro parte.

Fuchsia canescens sensu Munz, Proc. Calif. Acad. Sci. IV. 25:26. 1943, pro parte; Opera Bot., Ser. B, 3:12. 1974, pro parte.

Erect to scandent shrubs 0.4–3.5 m tall, sometimes semi-epiphytic on mossy tree trunks. Branchlets terete, 1.5–3 mm thick, densely hirsute to hirtellous or strigillose, usually with erect, white to tan hairs; older stems 3–10 mm thick with exfoliating bark. Leaves 3–5-verticillate, mostly ternate or quaternate, firmly membranous to subcoriaceous, narrowly to broadly elliptic to obovate, acute to obtuse at both ends, 2–5(–10) cm long, (0.6–)1–2.5(–4) cm wide, matte to subnitid green and usually strigose above, lighter green and hirsute to strigose below; secondary veins 3–8(–11) on either side of the midvein, often red below; margin subentire to denticulate. Petioles pubescent, 2–10(–20) mm long. Stipules narrowly lanceolate, 1.5–2.5 mm long, 0.3–0.7 mm wide, deciduous. Flowers generally fewer than 12 per branch, axillary and pendant. Pedicels pubescent, 5–25(–40) mm long. Ovary ovoid-ellipsoid, strongly tetragonous, 6–9 mm long, 2–3.5 mm thick, hirsute to strigose, green to dull red. Floral tube narrowly funnelform, (32–)36–50(–60) mm long, 3–4 mm wide and somewhat bulbous at the base, narrowed to 2–3.5 mm wide above the nectary, then gradually widened or slightly ampliate near the middle until 6–10 mm wide at the rim, hirsute to strigose or subglabrous outside, pilose inside for most its length. Sepals (narrowly) lanceolate, acute to subacuminate at the apex, (10–)13–20(–23) mm long, 3.5–5 mm wide, spreading to divergent at anthesis. Tube and sepals subnitid scarlet, pink, or orange red, sepals sometimes dull, green-tipped. Petals red, orbicular to obovate or broadly elliptic, rounded to (broadly) acute at the apex, (8–)9–15 mm long, (6–)8–13 mm wide, spreading to divergent at anthesis. Nectary unlobed or shal-

lowly 4-lobed, 1.5–2 mm high. Filaments red, 8–12 mm and 6–9 mm long; anthers oblong, 3–4 mm long, 1.5–2 mm wide, cream. Style red, villous for most its length; stigma conic-globose, slightly 4-cleft apically, 2–3.5 mm long, 1.5–4 mm wide, red. Berry tetragonous before maturity, subglobose to ellipsoid when ripe, 11–15 mm long, 7–9 mm thick, red purple; seeds tan, 1.8–2.5 mm long, 0.9–1.2 mm wide. Gametic chromosome number $n = 11(?)$, 22.

Distribution: Southern Colombia and Ecuador. Along the Cordillera Occidental from Nariño, Colombia to Cotopaxi, Ecuador, in elfin forest near tree line, 3,400–4,000 m; on the Cordillera Central (eastern escarpment of the Ecuadorian Andes) from Napo to Chimborazo, from tree line at 3,900 m to 2,500 m in cloud forest; and in the mountains of Azuay and Cañar from tree line to upper cloud forest, 2,850–3,400 m (Fig. 59).

Representative specimens examined: COLOMBIA, NARIÑO: Volcán Azufral, *André s.n.*, (K); Volcán Galera, near Pasto, *Barclay 4637* (COL); La Laguna, Mun. Cumbal, *Benavides 993* (PSO); NW slopes Volcán Chiles, *Ewan 16093* (POM); Volcán Cumbal, *Vogel 259* (U), *von Sneidern in 1941* (S). ECUADOR, AZUAY: Páramos de Silván, *Barclay & Juajibioy 8403* (RSA); 13–18 km from Cuenca on road past Sayausí, *Berry & Escobar 3184* (MO), *3187* (MO, QCA), *3188* (MO); 35 km S of Cuenca on road to Oña, *Berry & Escobar 3190* (MO, QCA); along Río Yanucay above San Joaquín, road to Laguna Soldado, *Berry & Escobar 3212* (MO, QCA), *3213* (MO), *3214* (MO), *3225* (MO, QCA); Yanasacha, Parroquia Baños, *Boeke 621* (MO); road Cuenca-Angas, near Angas, *Boeke 654* (MO); Páramo de Tinajillas, 30–50 km S of Cuenca, *Camp E-462* (NY, RSA), *E-2107* (NY, RSA), *E-2108* (NY, RSA); along Río Matadero, W of Cuenca, *Camp E-1988* (NY, RSA, U); N of Paute, *Camp 2590* (NY, RSA, VEN); 1–8 km N of Sevilla de Oro, *Camp 4257* (NY, RSA), *E-4672* (COL, G, MO, NY, P, RSA, S, US, VEN); Quebradas of the Río Collay, 3–8 km N of Sevilla de Oro, *Camp 4994* (G, MO, NY, RSA, UC, US); El Pan, *Harling 1228* (NY, S); 10 km S of Cumbe, *Harling 5658* (NY, S); 10–12 km N of Sevilla de Oro, *Øllgaard & Balslev 9366* (AAU, MO), *9374* (AAU, MO); near Laguna Sorocucho, *Prescott 827* (DS, NY), *Scolnik 1461* (RSA); Río Machangara, *Sparre 18561* (S), *18601* (S), *18664* (S). CAÑAR: above Biblián on road to Cañar, *Berry & Escobar 3227* (MO, QCA), *3228* (MO, QCA), *Harling 6296* (NY, S), *Harling et al. 8614* (RSA). CARCHI: Páramos del Angel, near Voladero, *Barclay & Juajibioy 9396* (RSA), *Penland & Summers 915* (F, GH, POM); base of Volcán Chiles, ca. 12 km W of Tufiño, *Berry 3156* (MO, QCA), *Øllgaard & Balslev 8398* (AAU); near El Angel, *Popenoe 1260* (NA); Páramo El Angel, *Sparre 14148* (S). CHIMBORAZO: Cordillera Oriental, between Alao & Cushnipaccha, *Acosta Solis 7201* (F), *7214* (F). COTOPAXI: 17 km above Pilaló, road to Latacunga, *Berry & Berry 2539* (MO), *2540* (MO); timberline on Pilaló-Latacunga road, *Holm-Nielsen & Jeppesen 1396* (AAU, S), *Holm-Nielsen et al. 3335* (AAU, S). IMBABURA: Laguna de Mojanda, *Øllgaard & Balslev 8779* (AAU). NAPO: between Oyacachi and Comenia, *Acosta-Solis 11166* (F); Cuyuja, *Balslev & Madsen 10469* (AAU), *10522* (AAU); ca. 5 km above Papallacta to Quito, *Berry & Berry 2521* (MO); Km 215 of Quito-Baeza road just above Lago Papallacta, *Berry & Berry 2523* (MO); 2–6 km below Papallacta, *Berry & Berry 2525* (MO), *2526* (MO), *Gentry 12401* (MO, US); just above town of Papallacta, *Berry & Escobar 3245* (MO); Lago San Marcos, E of Cayambe, *Cazalet & Pennington 5312* (NY, UC, US); Quebrada Chalpichio, ca. Km 204 E of Papallacta, *Croat 49412* (MO); Los Corrales, near Papallacta, *Grubb et al. 208A* (NY 2 sheets); below Papallacta, *Harling 3994* (NY, S); 4 km W of Papallacta, *Holm-Nielsen et al. 6785* (AAU, MO, NY, S); between Cuyuja and Papallacta, 10 km E of Papallacta, *Holm-Nielsen et al. 6834* (AAU, NY, S); Laguna de Papallacta, *Øllgaard & Balslev 8036* (AAU); ca. 7 km W of Papallacta, *MacBryde & Dwyer 1240* (MO, QCA); just W of Papallacta, *Plowman et al. 3870* (GH, K, MO, S); Río Papallacta, Station IV, *Prescott 1276* (MSC); Dos Arroyos, ca. 5 km NW of Laguna Norte de Papallacta, *Sparre 15021* (S); Río Calpi on Baeza-Papallacta road, *Sparre 15949* (S); Papallacta, *Sparre 17704* (S). PICHINCHA: E part of Haciendas Pedregal and Yanurcu, Chaparro de Sebritana, *Acosta-Solis 8353* (F); NW side of Volcán Pichincha, Yanacocha trail, *Luteyn et al. 5685* (MO). TUNGURAHUA: Llanganati mountains, ridge between Río Tope and Río Golpe, *Edwards 164* (K); Páramo de Minza, Minza Chica, *Penland et al. 337* (F, GH, POM).

Probable hybrids *Fuchsia vulcanica* × *F. ampliata*: ECUADOR, COTOPAXI: above Pilaló, 2,800 m, *Barclay & Juajibioy 8076-A* (RSA); 13 km above Pilaló on Quevedo-Latacunga road, ca. 3,300 m, *Berry & Berry 2541* (MO), *2542* (MO), *2543* (MO), *2544* (MO), *2545* (MO), *2546* (MO), *2547* (MO);

12 km E of Pilaló, *Escobar 1100* (MO); Prov. Cotopaxi, *Gilmartin 44* (MO); Pilaló-Latacunga road at timberline, 3,400 m, *Holm-Nielsen & Jeppesen 1396* (DS), *1397* (AAU, DS); Quevedo-Latacunga road, above Pilaló, 3,200–3,300 m, *Holm-Nielsen et al. 3268* (COL, MO, NY, S).

This species is part of the high elevation *Fuchsia petiolaris* species group of the northern Andes. It and *Fuchsia ampliata* are closely related and distinct from the other species in their generally rotund petals and coarse, usually dense pubescence. *Fuchsia vulcanica* can be distinguished from *F. ampliata* by its non-reflexed sepals, strongly tetragonous ovaries, smaller leaves, and shorter petioles and pedicels.

Fuchsia vulcanica is treated here as a widely polymorphic species. Intensive field work and cytological examination of more populations is badly needed and may in the future lead to the recognition of additional taxa, but the extent of variation within most parts of the range is such that no consistent morphological differences can be found to separate distinct taxa at this time.

The most uniform populations occur around the type locality in southern Colombia and northern Ecuador, where plants are all densely hirsute, with leaves less than 35 mm long, and pedicels less than 8 mm long. These plants occur only at or near treeline on the upper slopes of volcanic peaks. A possible diploid count of $n = \text{ca. } 11$ was obtained from this area from *Berry 3156*. Along the same mountain range, but further south in Imbabura and Pichincha, plants are found with shorter, hirtellous pubescence and slightly larger leaves 3–6 cm long.

The southernmost populations from Azuay and Cañar are apparently all tetraploid. Four tetraploid counts were obtained from two different populations (see Table 4). In addition, triplicate pollen grains, which often indicate polyploidy in the genus, have been found in representatives of different localities in this area, including *Harling 1228* (NY, S; El Pan), *Berry & Escobar 3225* (MO, QCA; above San Joaquín, road Cuenca-Laguna Soldado), *Øllgaard & Balslev 9374* (AAU, MO; 10–12 km N of Sevilla de Oro), and *Harling et al. 8614* (RSA; between Biblián and Cañar). Most plants from Azuay have somewhat smaller and thinner flowers than those found in the northern Provinces. Pubescence varies widely in these populations from densely hirsute to hirtellous, and the petals are particularly variable, from orbicular to elliptic and acute-tipped.

The type of *F. hitchcockii* is unusual in its long floral tubes (ca. 60 mm long). It represents the extreme of variability in this group, with petals half as long as the sepals and pedicels 3–4 cm long. Its hirsute pubescence and round petals are characteristic of *F. vulcanica*, however, and other collections from the same area are variable, but generally closer to the average values of morphological characters for this species.

There are two areas where *F. vulcanica* intergrades extensively with *F. ampliata* or else shows a great deal of polymorphism over an altitudinal gradient. In the Cordillera de Zumbagua, above Pilaló in Prov. Cotopaxi, *F. vulcanica* is found locally near treeline, ca. 3,450–3,500 m, and *F. ampliata* has been found in cloud forest around 2,850 m, but both are infrequent. In between, a wide range of intermediate forms were found; these collections are listed separately at the end of the specimens citation as probable hybrids of *F. vulcanica* $\times$ *F. ampliata*. In July 1977, *Berry & Berry 2541* to *2547* were collected from a rock pile that had been made by roadbuilding machinery. This population appeared to be a

hybrid swarm between the above two species, as shown by the wide variation in the degree of sepal reflexion, leaf size and texture, and pubescence. No significant reduction in pollen stainability occurs in the intermediate forms, however, which seems to confirm the close affinity of these two species. In 1979, two years after the initial visit, this population had been destroyed by road cleaning crews. Such repeated disturbance and rapid turnover of local populations and the tendency of *F. ampliata* to grow in higher and drier sites than the Zumbagua cloud forest are likely major factors in the probable breakdown of isolating mechanisms between *F. vulcanica* and *F. ampliata* in Cotopaxi.

The second area where considerable variability involving *F. vulcanica* occurs is in Napo, on the road from Quito to Baeza on the eastern slopes of the Andes. Typical, small-leaved, high elevation forms of *F. vulcanica* occur about 5 km above the town of Papallacta near treeline at 3,700 m. As one descends first to the town of Papallacta at ca. 3,300 m, then down as low as 2,500 m in cloud forest to the east of Papallacta, considerably larger leaved plants are found along with greater variability in pedicel length and degree of sepal reflexion. *Berry & Berry* 2528 (MO; ca. 12 km east of Papallacta, 2,600 m) is the extreme of leaf variation, with blades 10 cm long and 4 cm wide, with 9 secondary veins on each side of the blade. *MacBryde* 875 (MO; W end of Lago Papallacta, 3,300 m) has some pedicels 4 cm long and floral tubes 10–13 mm wide at the rim, both beyond the normal range of variability for *F. vulcanica*. All these collections share the 3–4-verticillate, short-petiolate leaves, hirtellous pubescence, and round petals of *F. vulcanica*, however. *Asplund* 18239 (S; Papallacta, 3,000 m) is a large-leaved form that apparently has reflexed sepals. This points to possible introgression with *F. ampliata*, but that species is not known from the eastern slopes of the Andes in Ecuador. A gametic chromosome count of $n = \text{ca. } 22$ was obtained from *Berry & Escobar* 3245 (MO, QCA; Papallacta). More intensive sampling and cytological study of plants from this area will be necessary to understand the dynamics of these populations better.

Besides *F. ampliata*, *F. vulcanica* occurs sympatrically with *F. loxensis* in Azuay and with *F. pallescens* at its lower altitudinal limits in Napo.

- 27. *Fuchsia ampliata*** Benth., Pl. Hartw. 178. 1845. Baill., Hist. Pl. 6:467, fig. 439. 1877. Hook., Bot. Mag. t. 6839. 1885. TYPE: Ecuador, Prov. Pichincha, slopes of Volcán Pichincha, ca. 3,000 m, 1841–1843, *Theodor Hartweg* 988 (K Benth. Herb., holotype; photograph, MO; BM, BR, BREM, CGE 2 sheets, F, G, K Hooker Herb., OXF, P, W 2 sheets, isotypes). Fig. 23.

Fuchsia ayavacensis sensu Munz, Proc. Calif. Acad. Sci. IV. 25:32, pl. 3, fig. 18. 1943, pro parte; Opera Bot., Ser. B, 3:12. 1974, pro parte.

Fuchsia canescens sensu Munz, Opera Bot., Ser. B, 3:12. 1974, pro parte.

Erect to scandent shrubs 1–3 m tall with mostly ascending branches. Young growth conspicuously canescent to hirtellous with white hairs; branchlets 2–3 mm thick, hirtellous to densely strigose, green to dull purple; older branches dull ash gray. Leaves ternate or occasionally quaternate, often drooping, membranous, (narrowly) elliptic to lanceolate, acute to narrowly cuneate at the base, acute to subacuminate at the apex, 4–9(–12) cm long, 1.5–4 cm wide, matte green

and strigose above, pale green and strigose-villous below with red purple veins; secondary veins 5–9(–11) on either side of the midvein; margin subentire to denticulate. Petioles strigose, 7–20 mm long, usually dull purple. Stipules lance-linear, 3–5 mm long, 0.5–1 mm wide, subpersistent. Flowers axillary and pendant, generally few. Pedicels stout, 1–2 mm thick, 15–35(–50) mm long, strigose. Ovary ovoid, usually constricted near the apex, 6–8 mm long, 3–4 mm wide, canescent-hirtellous and slightly furrowed. Floral tube funnelform, usually dilated above the middle, (32–)40–50(–65) mm long, 3–4.5 mm wide and bulbous at the base, tapered to 2–3(–4) mm wide in lower $\frac{1}{3}$, widened above until (6–)8–14 mm wide at the rim, strigose outside, villous inside for lower $\frac{1}{2}$ – $\frac{3}{4}$. Sepals lanceolate, narrowly acute at the apex, 16–23(–28) mm long, 6–8 mm wide, with a narrow, tapered tip in bud, fully reflexed soon after anthesis. Tube and sepals bright scarlet to orange red. Petals red to orange red, rotund to orbicular or very broadly ovate, (10–)13–18 mm long, (9–)10–16 mm wide, rounded to obtuse at the apex, erect to suberect at anthesis. Nectary green, shallowly 4–8-lobed, ca. 2 mm high. Filaments red or orange, 10–18 mm and 8–13 mm long; anthers oblong, ca. 4 mm long, 2–3 mm wide, cream. Style red, densely villous from the base to the rim of the tube; stigma globose to subclavate, slightly 4-cleft apically, 2–4 mm long, 2–4 mm wide, red. Berry ellipsoid, usually $\pm$ tetragonous before maturity, slightly verrucose, 14–16 mm long, ca. 8 mm thick, red; seeds tan, 1.8–2.1 mm long, 0.8–1.2 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuador, along the Cordillera Occidental from Imbabura to Bolivar and one collection from the Nariño-Putumayo border in southern Colombia; shrubs in hedgerows on dry slopes, near streams or in upper elevation cloud forest, (2,850–)3,000–3,500 m (Fig. 60).

Representative specimens examined: COLOMBIA, PUTUMAYO: S side of Laguna La Cocha, Páramo de Santa Lucía, source of Río Alisales, *Cuatrecasas 11884* (COL). ECUADOR, BOLIVAR: Simiatug, Hacienda Talahua, *Penland et al. 623* (F, GH, POM). COTOPAXI: Quevedo-Latacunga road, above Pilaló, 2850 m, *Holm-Nielsen et al. 3274* (AAU, NY, S). IMBABURA: Bosque Andino "Rosaspamba," E side of Mojanda, *Acosta-Solis 8104* (F); ca. 8 km W of Laguna Cuicocha on road to Intá, *Berry 3169* (MO, QCA); ridge of Moinala, SW of Volcán Cotacachi, *Owenby 2646* (COL, MO, RSA, US). PICHINCHA: Corazón, *André K.819* (F, K, NY); ca. 9 km W of Chillogallo to Chiriboga, *Berry & Escobar 3234* (MO, QCA); Pichincha, *Jameson in 1851* (BM, CGE, G, OXF, US), *Humboldt & Bonpland 3115* (F, P); Volcán Pichincha, *Mexia 7654* (BH, UC, US); road from Cotocollao, near Nono, *Mexia 7661* (BM, GH, K, MO, NY, POM, S, U, UC, US).

This species can be easily recognized by its broad, firm-tubed flowers with nearly erect, round petals and fully reflexed sepals at anthesis. The plants are generally covered by a tomentum of white, strigose-villous hairs, and the styles are densely pilose up to the rim of the tube. *Fuchsia ampliata* is a member of the high elevation *F. petiolaris* species group and was confused by Munz (1943, 1974) with *F. ayavacensis* from northern Peru and southernmost Ecuador. The differences between these two species are outlined under *F. ayavacensis*. *Fuchsia ampliata* largely is restricted to areas near tree line in a small extension of the Cordillera Occidental in central Ecuador, mostly on the drier eastern slopes facing the Central Valley of Ecuador. One disjunct collection is known from the eastern slopes of the Cordillera Central in southern Colombia, however. In Cotopaxi, Ecuador, above Pilaló, it occurs in moister cloud forest but is apparently quite rare. There, it hybridizes extensively with the closely related *F. vulcanica*, pro-

ducing local hybrid swarms. These are discussed more fully under *F. vulcanica*. *Fuchsia ampliata* also occurs sympatrically with *F. dependens* and *F. sessilifolia* in a few localities.

- 28. *Fuchsia venusta*** Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 6:105. 1823. Planch., Fl. Serres Jard. Eur. 5: t. 538. 1849; Rev. Hort. III. 4:241, t. 1850. Moore & Aynes, Gard. Mag. Bot. 2:36, fig. 2. 1850. Lindl. & Paxt., Paxton's Fl. Gard. 1:79, fig. 57. 1850. Anon., J. Hort. Pract. Gard. III. 49:243, t. 1904. *Fuchsia venusta* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25:39, pl. 5, fig. 26. 1943. Based on *F. venusta* HBK. TYPE: Colombia, Dept. Cundinamarca, near Guayavalito, July–Sept. 1801, *Alexander von Humboldt & Aimé Bonpland* (P, holotype, not seen; photographs, F, GH; microfiche, MO; P, isotype). Fig. 24.

Fuchsia killipii I. M. Johnston, Contr. Gray Herb. 81:94. 1928. Munz, Proc. Calif. Acad. Sci. IV. 25:52, pl. 8, fig. 41. 1943. TYPE: Colombia, Dept. Santander, Río Suratá, above Suratá, 2,000–2,300 m, 5–6 Jan. 1927, *Ellsworth P. Killip & Albert C. Smith* 16695 (GH, holotype; photographs, POM, UC; NY, US, isotypes).

Fuchsia venusta var. *huilensis* Munz, Proc. Calif. Acad. Sci. IV. 25:39. 1943. TYPE: Colombia, Dept. Huila, Cordillera Oriental, E of Neiva, 1,800–2,300 m, 1–8 Aug. 1917, *Henry H. Rusby & Francis W. Pennell* 874 (NY, holotype; photographs, POM, UC; F, GH, MO, US, isotypes).

Fuchsia meridensis Steyermark, Fieldiana Bot. 28:439. 1952. TYPE: Venezuela, Edo. Mérida, between La Azulita and La Trampa, road to Lagunillas, 1,280–2,285 m, 27 Aug. 1944, *Julian A. Steyermark* 56162 (F 1368909, holotype; NY, isotype).

Erect to scandent shrubs 1–3 m tall or lianas to 10 m above ground, with suberect or long, flexuous-pendant branches to several m long. Branchlets terete to subtriangular, 2–6 mm thick, minutely puberulent to finely hirtellous, dull wine red to bluish purple; older branches 10–40 mm thick, with tan, exfoliating bark. Leaves ternate, rarely opposite or quaternate, firmly membranous to subcoriaceous, elliptic, rounded to acute at the base, acute to subacuminate at the apex, 5–11.5 cm long, 1.5–4.5 cm wide, glossy dark green and subglabrous above, glossy pale green and subglabrous to pubescent along the nerves below; secondary veins 7–12 on either side of the midvein, impressed above, subelevated below; margin subentire. Petioles puberulent or strigillose, 4–10(–12) mm long, wine red. Stipules lance-deltoid, 1–1.5 mm long, ca. 0.4 mm wide, subulate at the apex, deciduous. Flowers axillary in uppermost leaf axils or subracemose at branch tips; when subracemose, rachis 2–4 cm long, subtending leaves usually deciduous. Pedicels slender to filiform, ascending to divergent in bud, arching or drooping by anthesis, (10–)15–30(–60) mm long, glabrous to pubescent. Ovary oblong to ellipsoid, 4–8 mm long, 2–3 mm thick. Floral tube narrowly funnelform, (30–)35–60 mm long, 2.5–4.5 mm wide and slightly bulbous at the base, narrowed to 2–4 mm wide above the nectary and gradually widened above until 5–10 mm wide at the rim, subglabrous to puberulent outside, pilose inside for most of length. Sepals lanceolate, 14–20 mm long, 4–7 mm wide, acute to acuminate at the apex, sometimes pubescent within, subulate in bud for 1–2 mm, spreading to divergent at anthesis. Tube lustrous orange red, at times greenish in bud; sepals orange red, often green-tipped in bud. Petals orange to orange red, oblanceolate, 15–22 mm long, 3–6 mm wide, undulate to crispate-margined, abruptly acute at the apex, strongly spreading and recurved at anthesis, with dorsal hairs occasionally pres-

ent along the midvein. Nectary green, unlobed to shallowly 4-lobed, ca. 2 mm high. Filaments light red, 10–15 mm and 8–11 mm long; anthers oblong, 2.5–3.5 mm long, 1.5–2 mm wide, cream to pale yellow. Style densely villous from the base to the rim of the tube, light red; stigma subglobose, 4-cleft apically, 2–3 mm long, 2–3 mm wide, dull white to orange red, exserted 3–15 mm beyond the anthers. Berry ellipsoid-oblong to subglobose, 8–20 mm long, 6–10 mm thick, lustrous dull green to dark purple; seeds tan, 1.5–2 mm long, 0.8–1.5 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia and Venezuela. Locally frequent to scattered shrubs or lianas along forest edges, streamsides, thickets or in trees of mid-elevation cloud forest; in Venezuela, from Mérida to Táchira; in Colombia in the Cordillera Oriental from Santander to Huila, and in the Cordillera Central in Tolima; 1,800–2,700 m (Fig. 60).

Representative specimens examined: VENEZUELA, MÉRIDA: La Carbonera, *Aristeguieta* 2847 (NY, VEN); La Loma de la Vagabunda, near El Morro, between El Morro and Aricagua, *Badillo* 6563 (MY); Quebrada de La Mucuy, towards El Volcán, *Bernardi* 280 (MER, NY); La Mucuy, *Bernardi* 306 (MER, NY, VEN); Alto de Monte Zerpa, *Bernardi* 664 (NY); El Paramito, between Mérida and La Carbonera, *Berry & Dugarte* 2507 (MER, MERF, MO), *Berry* 3450 (MO, VEN); ½ km below La Trampa, *Berry & Centeno* 2511 (MER, MERF, MO); 23 km above La Azulita on road to La Trampa, *Berry & Centeno* 2512 (MER, MERF, MO); 17 km E of Zumbador to Queniquea, *Berry* 3422 (MO, VEN); La Mucuy to Mesa de los Pinos, *Berry* 3431 (MO, VEN), *Berry in* 1980 (MO), 3433 (MO, VEN); 3–5 km below San Eusebio, road to La Azulita, *Berry* 3542 (MO, VEN), 3455 (MO); Páramo de Aricagua, *Jahn* 1029 (GH, US, VEN); Chorrera de La Gonzales-La Isla-Jají, *López-Palacios* 1919 (MERF, MO); El Chorotal, *Quintero* 1614 (MER); El Valle Grande, between San Javier and la Sierra de la Culata, *Ruiz-Terán & López-Figueiras* 2116 (MERF, MO); El Yagrumal, above El Maciegal, ca. 10 km W of Mérida, *Ruiz-Terán et al.* 12540 (MERF, MO); Bosque Experimental de San Eusebio, *Wessels-Boer* 1733 (MER, MO, U, VEN). TÁCHIRA: 21 km E of El Portachuelo to Pregonero, *Berry* 3292 (MO, VEN); 13 km E of Zumbador, *Berry* 3302 (MO, VEN); 11–17 km W of Zumbador towards San Isidro, *Bunting* 2564 (MY); Páramo el Pantano, *Charpin et al.* 13459 (G); Páramo del Zumbador, *Ferrari* 1171 (MY); Páramo de Angaraveca, *Jahn* 129 (US, VEN); between Michelena and Boca de Monte, W of Zumbador, *Steyermark & Rabe* 96805 (NY, U, VEN); 4.5 km above El Hato, ca. 30 km above Pregonero on road to Bailadores, *Tillett & Hönig* 758-520 (MO). COLOMBIA, BOYACÁ: Chiquinquirá, *Ariste-Joseph* A842 (US); Yanaca-Mapiri, *García-Barriga* 4911 (COL, US); near Socotá, Sierra Nevada del Cocuy, *Grubb et al.* 697 (COL, K); Km 307 above Pajarito, Rancherías, *Idrobo & Jaramillo* 1605 (COL); near Quebrada Chorro Grande, N side Arcabuco Range, between Duitama and Charalá, *Langenheim* 3614 (COL, UC, US); Finca La Saria, Corregimiento de Virolín, *Lozano et al.* 2393 (COL); Km 88 road to Pajarito, Quebrada La Rocha, *Sastre* 733 (COL, MO, P); road to Barbosa, 10 km NW of Arcabuco, *Steere* 7048 (BH, COL, MICH); above Corinto, road Pajarito-Sogamoso, *Uribe-Uribe* 6534 (COL); Tota, *Yepes-Agredo* 3339 (COL). CUNDINAMARCA: Quebrada Honda, *André in* 1876 (K); Facatativá, *Ariste-Joseph* A514 (US); ca. 2.5 km W of Salto de Tequendama, road to El Colegio, *Barclay et al.* 3305 (COL, NA, US); just below Zipacón, *Berry* 3540 (COL, MO); Km 39 of Bogotá-Sibaté-Fusagasugá road, *Berry* 3548 (COL, MO); 10 km above Choachí, *Breedlove* 35540 (CAS); Salto de Tequendama, *Cuatrecasas* 48 (COL, F, US); Boca de Monte, *Cuatrecasas et al.* 25816 (COL); Tena, *Dawe* 23 (K, US); Choachí, *Dawe* 350 (K, US); San Miguel and Aguabonita, *Duque-Jaramillo* 3323 (CM, COL); Laguna Pedro Palo, 3 km N of Tena, *Fernández & Mora* 1449 (COL); 5 km NNW of Cabrera, N and W of Río Sumapaz, *Fosberg* 20982 (RSA, US); 12 km WSW of Junín, on Río Blanco, drainage of Río Sueva, *Fosberg* 21479 (NY, RSA, UC, US); 21482 (RSA, US); 5 km WSW of Charquito, headwaters of Río Subia, *Fosberg* 22038 (NY, RSA, US); between Pacho and Río Negro, *García-Barriga* 10754 (COL, US); Sasaima, La María, *García-Barriga* 12584 (COL, POM, US); Km 18 of road Mosquera-La Mesa, *Gentry* 17050 (COL, MO); 12 km NW of Gachetá, Moquentina valley, *Grant* 9534 (NA, RSA, US); San Fortunato, *Hartweg* 995 (BM, BREM, CGE, F, G, K, LE, NY, OXF, P, W); Zipaquirá-Pacho highway, *Haught* 5979 (COL, POM, US); Fómeque, toward the Páramo de Chingaza, *Huertas & Camargo* 5536 (COL); Junín, Vereda La Cumbre, toward Claraval, *Huertas & Camargo* 6602 (COL); above La Florida, *Idrobo & Jaramillo* 2250 (COL); Las Mercedes, *Lourteig* 3082 (MO); between Agua Larga and Facatativá, *Mayor* 56 (Z); Dintel, *Pérez-Arbelaes & Cuatrecasas* 5291 (F, COL); Zipacón, *Popenoe* 1056 (NA); Santandercito-La Rambla, *Silva & Moreno* 270 (COL); Santandercito, *Uribe-Uribe* 1020

TABLE 11. Distinguishing characters of *Fuchsia gehrigeri* and *F. venusta*.

	<i>F. gehrigeri</i>	<i>F. venusta</i>
Twig color	Light red to green	Wine red
Leaf surface	Matte	Glossy
Leaf texture	Membranous	Firmly membranous to subcoriaceous
Leaf margin	Denticulate	Entire
Petiole length	10–40 mm	4–10 mm
Flower color	Red	Orange red
Petal surface	Smooth	Undulate
Fruit shape	Ovoid-globose	Ellipsoid
Seed length	2–3 mm	1.5–2 mm

(COL, U); Pacho, *Uribe-Uribe 1718* (COL). HUILA: Batán, on Río Neiva, ca. 32 km SE of Neiva, *Fosberg 19296* (NY, RSA); Quebrada Ariari, above Galilea, 23 km ENE of Colombia, *Fosberg 19625* (RSA, US); Yucales, on Río Fortalecillas, 32 km E of Neiva, *Fosberg 19744* (RSA, US); E of Neiva, *Rusby & Pennell 641* (GH, MO, NY, US); Balsillas, on Río Balsillas, *Rusby & Pennell 722* (GH, NY, US). SANTANDER: La Baja, *Funck & Schlim 1306* (BM, CGE, F, G, LE, OXF, P, W); above Suratá, *Killip & Smith 16604* (A, US); vicinity of La Baja, *Killip & Smith 16776* (A, F, GH, NY, S, US); vicinity of Charta, *Killip & Smith 18854* (A, GH, NY, US). TOLIMA: 24 km W of Fresno to Manizales, *Berry 3551* (COL, MO); between Líbano and Murillo, *Escobar 1008* (MO); Líbano, *Pennell 3197* (GH, NY, US).

Fuchsia venusta is one of few species that often climb up trees, with its long, flexuous branches (Fig. 3). It also can grow as an upright shrub, however. It is distinguished by its ternate, short-petiolate, elliptic leaves that are glossy on both surfaces and the wine red to dull bluish purple stems. The flowers are axillary to subracemose, with orange tubes, green-tipped sepals, and recurved, undulate-crispate petals. It is closely related to *F. rivularis* from northern Peru. That species, however, has mostly quaternate leaves, more secondary veins, and mostly spreading sepal tips in bud. *Fuchsia gehrigeri* is another related species that is sympatric and can be confused with *F. venusta*; a list of their distinguishing characters is given in Table 11.

Considerable variation in pubescence, leaf texture, and amount of green coloration in the tube and sepals occurs between different populations of *Fuchsia venusta*. Along the edges of the Bogotá Plateau where this species is common, localized variation in the above characters is found. Plants near the Salto de Tequendama have subcoriaceous leaves and thick stems with erect, hirtellous pubescence, but populations nearby at Zipacón and Aguabonita on the old Bogotá-Fusagasugá road are typically subglabrous with membranous leaves. However, plants from opposite ends of the range, in Huila, Colombia and Mérida, Venezuela, often show little morphological differentiation.

Populations from northern Santander were described by Johnston as *Fuchsia killipii*. Compared to other populations of *F. venusta*, these plants have more numerous flowers in generally tightly clustered groups and smaller, globose fruits. I could not find populations from this area during field studies in Santander, but the cited collections appear to be localized variants of *F. venusta* because of their shrubby to climbing habit, ternate, glossy leaves, pilose styles, and the frequent hairs on the petals and sepals.

There are a few localized populations of *F. venusta* in Dept. Tolima on the

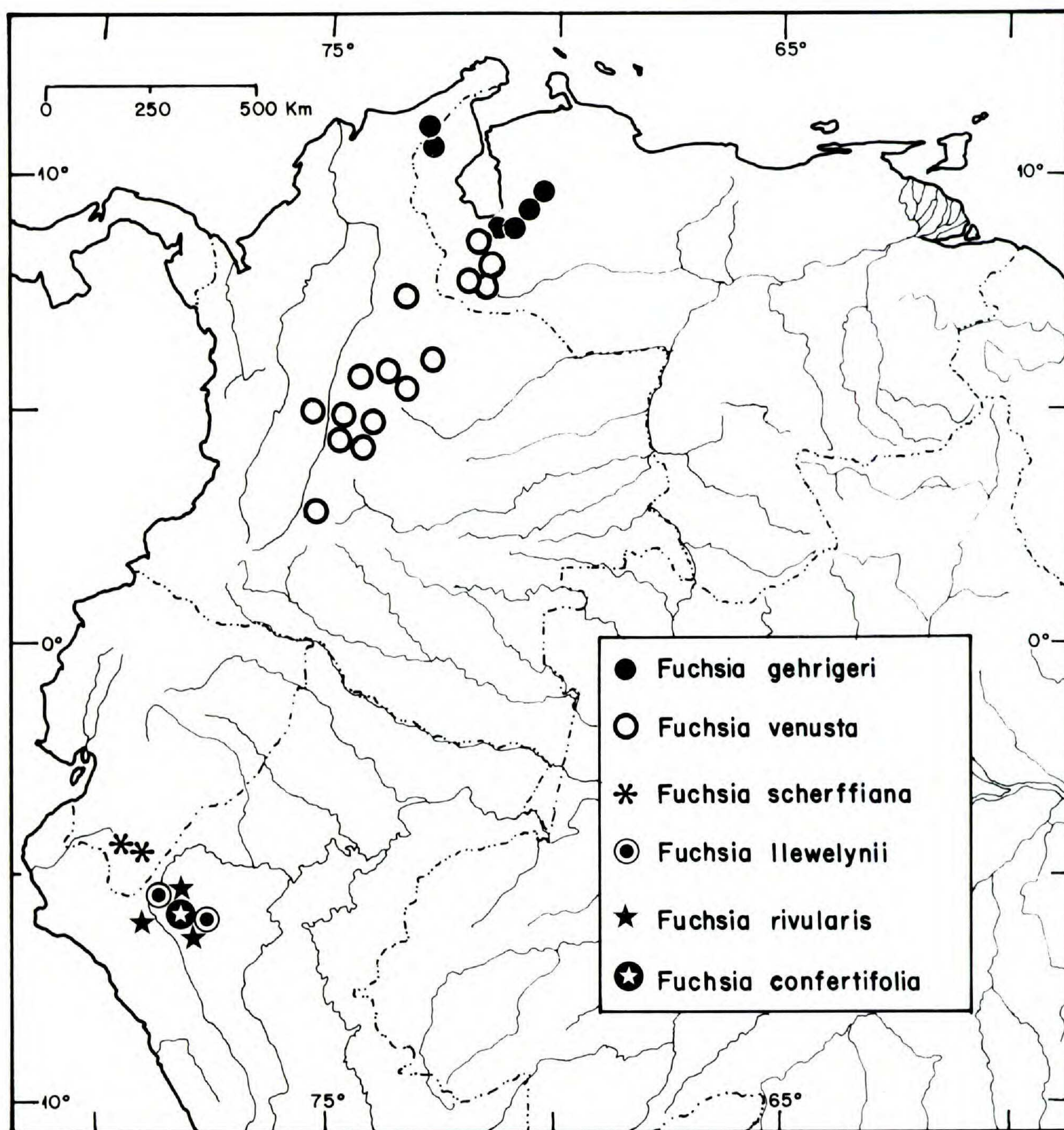


FIGURE 60. Distribution of the *Fuchsia venusta* species group.

eastern slopes of the Cordillera Central at the latitude of the Bogotá Plateau; plants probably spread there from the Cordillera Oriental, the same as with *F. hirtella*, *F. nigricans*, and *F. petiolaris*.

Fuchsia venusta occurs sympatrically with *F. gehrigeri*, *F. hirtella*, *F. nigricans*, and *F. verrucosa*. It apparently hybridizes with *F. gehrigeri* in Mérida and Táchira, Venezuela. Hybrids with *F. hirtella* were collected in Cundinamarca, Colombia, along the old Bogotá-Fusagasugá road. In both these cases, the putative hybrids occur at the upper altitudinal limit of *F. venusta* and the lower limit of *F. hirtella* and *F. gehrigeri* (Fig. 6). Hybrids between *F. venusta* and *F. nigricans* are relatively common in Venezuela. Further analysis of these hybrids is included in the discussion of *F. gehrigeri*, *F. hirtella*, and *F. nigricans*.

29. *Fuchsia rivularis* J. F. Macbride, *Candollea* 8:24. 1940; *Field Mus. Nat. Hist., Bot. Ser.* 13(4):562. 1941. Munz, *Proc. Calif. Acad. Sci.* IV. 25:27. 1943. TYPE: Peru, Dept. Amazonas, Chachapoyas, 1830–1841, *Andrew Mathews* (G-BOIS, lectotype, here designated; photograph, MO; G-DEL, isotype).

Fuchsia woytkowskii J. F. Macbride, *Field Mus. Nat. Hist., Bot. Ser.* 13(4):566. 1941. Munz, *Proc. Calif. Acad. Sci.* IV. 25:25, pl. 2, fig. 11. 1943. TYPE: Peru, Dept. Amazonas, Almirante, 1,900 m, *Felix Woytkowski* 38 (F, holotype; photographs, NY, UC).

Scandent shrubs or lianas to 10 m above ground, with long, flexuous-arcuate, mostly unbranched shoots to several m long. Branchlets and young growth subglabrous to puberulent, older branches pilose or puberulent, glabrescent with age, with subnitid, red purple bark exfoliating in wide strips. Leaves ternate or mostly quaternate, subcoriaceous, narrowly elliptic to elliptic, acute to obtuse at the base, narrowly acute to obtuse or subacuminate at the apex, 5–9 cm long, 2–5 cm wide, nitid dark green and subglabrous above, paler green and subglabrous to pilose below; secondary veins 13–15 on either side of the midvein, midrib elevated below; margin subentire to glandular-denticulate. Petioles stout, pilose, 3–6 mm long. Stipules triangular-lanceolate, 2–3 mm long, 0.8–1.3 mm wide, thick at the base, spreading, subpersistent. Flowers few and pendant in uppermost leaf axils. Pedicels drooping to subdivergent, puberulent, 10–53 mm long. Ovary cylindrical, 6–8 mm long, 2–3 mm thick, generally pubescent. Floral tube narrowly funnelform, 36–65 mm long, slightly bulbous at the base and 3–5 mm wide, narrowed to 2–4 mm wide above the nectary, then widened gradually above until (5–)6–10 mm wide at the rim, subglabrous to pilose or strigillose outside, pilose inside. Sepals narrowly lanceolate, 16–20 mm long, 3–7 mm wide, with mostly free, spreading tips in bud 1.5–2.5 mm long, divergent at anthesis. Tube and sepals bright scarlet. Petals orange red, oblong to lance-elliptic, 15–22 mm long, 4–7 mm wide, crispate-margined, often with a few, scattered hairs on the midvein dorsally, spreading-recurved at anthesis. Nectary light green, shallowly 4-lobed, 3–4 mm high, fused to the base of the tube in lower $\frac{2}{3}$. Filaments red, 10–15 mm and 6–11 mm long; anthers narrowly oblong, 4–4.5 mm long, 1.5–2 mm wide, white. Style red, usually glabrous; stigma subobconic, 3–4 mm long, 2–3 mm wide, lightly 4-cleft apically, light red. Berry ellipsoid, 14–16 mm long, 8–10 mm thick, reddish; seeds tan, 1.1–1.4 mm long, 0.8–1.0 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Locally frequent in thickets, frequently climbing up trees in forest openings, in mid-elevation cloud forest of Dept. Amazonas, east and northeast of Chachapoyas, 2,100–2,600 m; a few collections are also known from Dept. Cajamarca, Prov. Cutervo, 1,900–2,650 m (Fig. 60).

Representative specimens examined: PERU, AMAZONAS: 9 km E of Molinopampa on Chachapoyas-Mendoza road, *Berry & Escobar* 3617 (MO, USM); Km 22 of Carretera Marginal E of Pedro Ruiz towards Rioja, *Berry & Escobar* 3626 (MO, USM); on road to Pomacochas, 28 km above Puente Ingenio, *Hutchison & Wright* 6778 (RSA, UC, USM); beyond Buenos Aires, Carretera Marginal, Dto. Yambasbamba, Prov. Bongará, *Tillett* 673-213a (VEN); Mendoza, *Woytkowski* 8202 (MO); hills WNW of Pomacocha, *Wurdack* 938 (F, NY, RSA, US). CAJAMARCA: Socata-San Andrés, *López & Sagástegui* 5372 (MO); Achira, near Socota, Prov. Cutervo, *Velarde Nuñez* 7065 (Z); El Suro, Prov. Cutervo, *Velarde Nuñez* 7022 (Z).

This species is closely allied to *Fuchsia venusta* on the Northern Andes, which also has the unusual climbing habit, purplish stems, firm, nitid, short-petiolate leaves, and the axillary flowers with crispate-undulate petals. *Fuchsia rivularis* differs from that species in its generally quaternate leaves, less divergent pedicels, more numerous secondary veins, and spreading sepal tips in bud. Its distribution is centered in the moist cloud forests of central Dept. Amazonas, but three collections were seen from across the Río Marañón valley in Dept. Cajamarca that differ in their denser, short pilose pubescence, obtuse leaf tips, pilose styles, and slender floral tubes only 5 mm wide at the rim. Further habit and habitat information on these plants is necessary, however, before we can decide if these are distinct enough to warrant separate taxonomic recognition.

Fuchsia rivularis is sympatric with *F. pilosa*, but the two differ markedly in habit, and no hybrids have been detected.

30. ***Fuchsia gehrigeri*** Munz, Proc. Calif. Acad. Sci. IV. 25:41, pl. 5, fig. 28. 1943. TYPE: Venezuela, Edo. Mérida, Mucurubá, slopes and banks of La Cañada Grande, right fork of the town's stream, 2,800–3,100 m, 14 July 1930, *Wilhelm Gehrig* 322 (US 1515306, holotype; F, G, GH, MO, NY, PH, VEN, isotypes).

Fuchsia jahnii Munz, Proc. Calif. Acad. Sci. IV. 25:40, pl. 5, fig. 27. 1943. TYPE: Venezuela, Edo. Mérida, Páramo de la Sal, 2,800 m, 2 Nov. 1921, *Alfredo Jahn* 506 (US 1186509, holotype; photographs, NY, POM; GH, VEN, isotypes).

Erect to usually scandent-climbing shrubs 2–5 m high, with arching-pendant branches. Young growth sparsely puberulent to subcanescent, rarely densely pilose; branchlets subterete, subglabrous to strigose (rarely reddish pilose); older stems 8–18 mm thick, long and flexuous if climbing, with tan, flaky bark. Leaves mostly ternate, occasionally opposite or quaternate, membranous, (narrowly) elliptic to slightly (ob-)ovate, acute to obtuse or attenuate at the base, acute to subacuminate at the apex, 3.5–12 cm long, 1.5–5 cm wide, deep matte velvety green and strigillose to subglabrous above, pale dull green to purplish and strigillose below, hairs denser along the veins; secondary veins 5–12 on either side of the midvein; margin usually denticulate. Petioles light red, 10–40(–48) mm long. Stipules lanceolate, 1.5–2 mm long, divergent-spreading with age, subpersistent. Flowers axillary and clustered at the branch tips or sometimes corymbose with a rachis 2–6 cm long; flowers, pedicels, and flowering branches pendant. Pedicels loosely strigose, 12–40 mm long. Ovary ovoid, 5–7 mm long, 2–4 mm thick, strigillose to pilose. Floral tube narrowly funnelform, 40–50(–55) mm long, (2.5)3–4 mm wide and bulbous at the base, narrowed to 2–3 mm for the basal 18–22 mm of the tube, then gradually or usually abruptly widened and 8–9 mm wide near the rim, subglabrous to puberulent-strigose outside (rarely pilose), (densely) pilose or villous inside in lower 2–4 cm. Sepals lanceolate, acute to acuminate at the apex, (13–)15–21 mm long, (4–)5–6 mm wide, spreading at anthesis. Tube and sepals subnitid red. Petals scarlet, oblong to elliptic-obovate or lanceolate, 14–21 mm long, (4–)6–8 mm wide, obtuse to acute at the apex, margin and surface smooth, often with several hairs on dorsal surface, spreading to slightly recurved at anthesis. Nectary unlobed or slightly 4-lobed, 1.5–2 mm high. Filaments light red, sometimes whitish at the base, 10–14 mm and 8–12 mm long; anthers oblong,

2.5–3 mm long, ca. 1.5 mm wide, white. Style red, glabrous to loosely villous; stigma subglobose, 2–2.5 mm long, ca. 2 mm wide, slightly 4-cleft at the apex, dull cream to pink red. Berry ovoid to subglobose, somewhat quadrangular before maturity, 13–16 mm long, 10–13 mm thick, dark red purple at maturity; seeds 2–3 mm long, 1.1–1.4 mm wide. Gametic chromosome number $n = 11$.

Distribution: Venezuelan Andes and the Serranía de Perijá along the Colombian-Venezuelan border; in the Mérida Andes, in Trujillo, Mérida, and Táchira; in the Sierra de Perijá in Zulia, Venezuela and Cesar, Colombia, 2,200–2,800(–3,100) m, in cloud forest thickets and woods (Fig. 60).

Representative specimens examined: VENEZUELA, MÉRIDA: vicinity of Piñango, La Pinita, *Badillo* 921 (VEN); between El Valle and Páramo La Culata, *Benítez de Rojas* 1523 (MY); bridge of Quebrada El Valle, 7 km above Hotel Valle Grande, *Berry & Ruiz-Terán* 2504 (MER, MERF, MO); Mucurubá, Quebrada El Rincón, above the town, *Berry & Ruiz-Terán* 2509 (MER, MERF, MO); above Piñango, 4 km below Las Pailitas, 43 km W of Pico El Aguila, *Berry* 3138 (MO, VEN); 9 km above Santo Domingo on road to Apartaderos, *Berry* 3139 (MO, VEN), 3310 (MO), 3599 (MO); Mesa de Los Pinos, above La Mucuy, *Berry* 3440 (MO, VEN), 3442 (MO), 3445 (MO, VEN); Páramo de Pinaño, *Jahn* 402 (US, VEN); Pueblo Llano, *López-Palacios* 53 (MER); trail from La Escalera to Puente de la Escalera, *Luteyn et al.* 6212 (MO); above Las Piedras, watershed of Río Aracay, *Ruiz-Terán et al.* 8238 (MERF, MO); between El Arbolito and El Alto, N of Piñango, *Ruiz-Terán & Dugarte* 12356 (MERF, MO); between El Chorrerón and La Cueva, road to Páramo de Palmita, *Ruiz-Terán & Dugarte* 12489 (MERF, MO), 12493 (MO). TRUJILLO: above Jajó, *Aristeguieta & Medina* 3397 (VEN); 12 km above and W of San Rafael on old Boconó-Trujillo road, *Berry* 3098 (MO, VEN); ca. 3 km S of Las Mesitas, at Visún, Río La Coneja, *Berry* 3128 (MO, VEN); 4–5 km along old Boconó-Trujillo road, 2 km S of lateral to Burbusay, *Tillett* 739-573 (MO). ZULIA: Campamento Frontera II, near international boundary, headwaters of Río Negro, Sierra de Perijá, *Tillett & Hönig* 746-678 (MO, VEN), 746-705 (MO, VEN), 746-766 (MO, VEN); Campamento Frontera V, on international boundary with Colombia, headwaters of Río Guasare, Sierra de Perijá, Serranía de Valledupar, *Tillett* 746-1033 (MO, VEN), 746-1086 (MO, VEN). COLOMBIA, CESAR: Sierra de Perijá, E of Manaure, Sabana Rubia, *Cuatrecasas & Romero Castañedas* 25061 (COL, RSA, US); Sierra de Perijá, E of Manaure, Quebrada de Floridablanca, *Cuatrecasas & Romero Castañedas* 25224 (COL, US).

This species is characterized by its thin, denticulate, and rather long-petiolate leaves; its smooth, elliptic-oblong petals with frequent hairs on the back, and the ovoid-globose fruits with large seeds 2–3 mm long. It resembles *Fuchsia venusta* in its subracemose flowers, similar floral dimension, and frequent hairs on the petals. Since the two occur sympatrically, a list of their distinguishing characters is presented in Table 11. It may also be related to *F. petiolaris* from Colombia, which has similar leaves, large seeds, and pubescent petals.

Considerable leaf and pubescence variation occurs within a small area in different populations of *F. gehrigeri*. Characters such as differing pedicel lengths, hair length, and sepal tip length, however, which Munz used to distinguish *Fuchsia jahnii* from *F. gehrigeri*, were shown by field studies conducted near both type localities and in intermediate areas to be too variable to be of any taxonomic importance.

Plants that are unusually pilose, with smaller flowers than most populations of *F. gehrigeri*, are found above the town of Santo Domingo on the road to Apartaderos in Edo. Mérida. The hairs on these plants are often gland tipped and become reddish with age. A typical, less pubescent and longer-tubed plant of *F. gehrigeri*, *Ruiz-Terán et al.* 8238 (MERF, MO) comes from a valley adjacent to Santo Domingo, however, indicating that the populations at Santo Domingo may be very localized variants.

Somewhat verrucose floral tubes and pedicels are found in populations north-

west of the city of Mérida, in the Valle Grande. These plants often have papillae protruding at the base of adjacent sepals. Some introgression may be occurring with *F. venusta*, because *Berry & Ruiz-Terán 2505* (MERF, MO; Quebrada Valle Grande, 7 km above Hotel Valle Grande) has morphological characters intermediate between the two species, such as smooth, elliptic petals of *F. gehrigeri* but subnitid, nearly entire leaves as in *F. venusta*. It has a pollen stainability of 66.8% (400 grains), compared to 94.7% (400 grains) for *Berry & Ruiz-Terán 2504* (MERF, MO), which is morphologically closer to *F. gehrigeri*. This valley has long been farmed and grazed by livestock, so these repeated disturbances may have led to an increased level of hybridization. In the same area, hybrids of *F. venusta* and *F. nigricans* are also found.

In contrast to El Valle Grande, populations of *F. gehrigeri* and *F. venusta* occur on virtually undisturbed slopes of primary cloud forest above La Mucuy, in the Parque Nacional Sierra Nevada, on the opposite side of the Río Chama from Mérida. There, a continual vegetation transect can be made following the trail from 2,250 m to 3,350 m at tree line (Fig. 6). *Berry 3439* (MO) was collected at 2,630 m and is apparently a hybrid between the lower elevational *F. venusta* and the mostly higher altitude *F. gehrigeri*. It has a low pollen stainability (31.5% of 400 grains) and the following intermediate morphological characters: subcoriaceous leaves, matte green above, but nitid below; petioles 8–20 mm long; and orange red flowers with smooth petals. *Bernardi 664* (NY; Edo. Mérida, Monte Zerpa, 2,600–2,800 m, June 1953) is another probable hybrid between *F. gehrigeri* and *F. venusta*. The floral tubes of this collection reach nearly 60 mm, and pollen stainability is 69% (1,000 grains examined).

An altitudinal separation similar to that of La Mucuy occurs further south in Edo. Táchira along the road from Zumbador to Queniquea. *Fuchsia venusta* is again the lower altitudinal species, occurring from 2,400–2,700 m on the eastern side of the ridge above Queniquea. *Berry 3295* (MO), *3296* (MO), and *3297* (MO, VEN; $n = 11$) occur at or just below the crest of the ridge, 4–6 km E of Zumbador, at 2,850–2,900 m, and resemble *F. gehrigeri* in their denticulate, long-petiolate leaves; the smooth, elliptic petals; and the ovoid-globose fruits with large seeds. The leaves tend to be broader and more ovate than the normal range of *F. gehrigeri*, however, and the sepals are strongly divergent, the branches ascending, and the floral tubes only gradually widened. Possible hybrids between these populations and *F. venusta* were collected on the east side of the ridge, 3 km E of Zumbador, at 2,760–2,775 m. *Berry 3414* (MO; $n = 11$) and *Luteyn et al. 5358* (NY) have unusually long floral tubes up to 78 mm long, elliptic, smooth petals, and subnitid, elliptic leaves with wine red stems. The floral tube length is greater than the extremes recorded in either *F. venusta* or *F. gehrigeri*, but the other characters are intermediate. Pollen stainability of *Berry 3414* is 69% (300 grains examined).

Fuchsia gehrigeri is also known to hybridize with *F. nigricans*, and the four putative hybrid collections are discussed under that species. It is also sympatric with *F. verrucosa*, but does not hybridize with that species.

A disjunct series of populations occurs in the Serranía de Perijá, along the Colombian-Venezuela border. The specimens from this area are very similar to those from the Mérida Andes except for the following differences: usually nar-

lower leaves with narrowly cuneate to attenuate bases, some petioles as long as 48 mm, more freely exfoliating bark, and generally more corymbose flowers. Petal shape varies in the few collections available from elliptic to lanceolate, but they are generally narrower, and the tips more acute, than plants from the main part of the range. None of the petals have dorsal hairs, however, which are usually found in populations from Mérida and Trujillo. More complete collections and additional field data from Perijá may in the future lead to the recognition of these populations as a separate taxon closely allied to *F. gehrigeri*.

31. *Fuchsia llewelynii* J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):556. 1941. Munz, Proc. Calif. Acad. IV. 25:38, pl. 5, fig. 25. 1943. TYPE: Peru. Dept. Amazonas, La Ventana, path from Chachapoyas to Moyobamba, among shrubs on exposed rocky slopes, 2,700–3,300 m, 21 Jan. 1930, *Llewelyn Williams* 7594 (F 626222, holotype; photographs, NY, UC).

Low shrubs with puberulent or canescent branchlets with spinescent projections, usually appearing papillose or verrucose when dry. Leaves opposite or ternate, membranous to subcoriaceous, narrowly oblong to elliptic or oblanceolate, acute at both ends, 2.5–9(–20) cm long, 1.2–4 cm wide, glabrous to strigillose on both surfaces; secondary veins 9–13(–25) on either side of the midvein; margin conspicuously dentate or serrulate. Petioles 3–9 mm long. Stipules narrowly lanceolate or filiform, 2–5 mm long, subpersistent. Flowers few and axillary at the branch tips or subracemose. Pedicels slender, puberulent, verrucose or with spinescent protuberances, 2–6 cm long. Ovary narrowly oblong, 5–6 mm long, ca. 1.5 mm thick. Floral tube cylindric-funnelform, (40–)45–54 mm long, slightly bulbous and 3–4 mm wide at the base, narrowed briefly to 2–3 mm wide above the nectary, then widened above until 5–8 mm wide at the rim, subglabrous to puberulent outside, pilose inside in lower $\frac{3}{4}$. Sepals narrowly lanceolate, acuminate, 13–17 mm long, 4–8 mm wide, with a tip ca. 2 mm long in bud. Tube and sepals dull pink. Petals pink, narrowly lanceolate to elliptic, acute to acuminate, 15–20 mm long, 4–8 mm wide. Nectary unlobed, ca. 2 mm high. Filaments 12–13 mm and 10–11 mm long; anthers oblong, 2.5–3 mm long, 1–1.5 mm wide. Style densely pilose for most its length; stigma subobconic, ca. 2 mm long, 1.5–2 mm wide. Berry ellipsoid, 12–15 mm long, ca. 8 mm thick.

Distribution: Northern Peru. Known from the mountains near La Ventana and Almirante, east of Chachapoyas and in the Serranía de Bagua, Dept. Amazonas, 2,600–3,300 m (Fig. 60).

Specimens examined: PERU, AMAZONAS: Cordillera Colán, SE of La Peca, Prov. Bagua, *Barbour* 3828 (MO); Almirante, *Mathews* 1480 (K, OXF); path between Chachapoyas and Moyobamba, *Weberbauer* 4437 (G).

This species is apparently very rare and localized, as evidenced by the few specimens collected. The leaves are mostly narrowly oblanceolate and conspicuously toothed, but the most characteristic features are the long pedicels and unusual stems, which have numerous papillose or spinescent projections. The flowers are borne subracemosely, and the petals are slender and more or less recurved, characters that ally it to *F. venusta* and *F. rivularis*.

32. **Fuchsia scherffiana** André, Rev. Hort. 60:233, 268. 1888. TYPE: Ecuador, Prov. Zamora-Chinchipe, Alto Cruz Grande (4°32'S, 79°02'W), 19 Nov. (?) 1876, Édouard André (K, holotype). This is probably an H. Poortman collection, since he collected for André in southern Ecuador after André returned to Europe in Sept. 1876 (L. B. Smith, pers. comm.).

Erect to scandent shrubs 0.5–3 m tall with spreading branches. Branchlets canescent-strigillose, terete, 1–2.5 mm thick, purplish; older stems 3–10 mm thick, dull purple. Leaves opposite or occasionally ternate, firmly membranous, (very) narrowly elliptic to narrowly lanceolate, acute at the base, acute to acuminate at the apex, 2.5–10 cm long, 0.8–2.3 cm wide, (very) dark nitid green and strigose above, shiny green to metallic purple and strigose with long villous hairs along the midvein below; secondary veins 6–10 on either side of the midvein; margin subentire to slightly revolute. Petioles strigose, purplish, 4–15 mm long. Stipules lance-linear, dark, 1–2 mm long, ca. 0.3 mm wide, subpersistent. Flowers few and axillary, pendant. Pedicels strigillose, 15–20 mm long. Ovary oblong, strongly tetragonous, 7–8 mm long, 1.5–2 mm thick, greenish. Floral tube narrowly funnelform, 44–50 mm long, 2.5–4 mm wide and slightly bulbous at the base, narrowed to 2–2.5 mm wide above the nectary, gradually widened above until 7–8 mm wide at the rim, sparsely strigose outside, villous inside in lower ½. Sepals lanceolate, acuminate, 12–14 mm long, 3.5–5 mm wide, spreading at anthesis. Tube and sepals orange red. Petals red, narrowly elliptic-lanceolate, (narrowly) acute at the apex, 9–11 mm long, 3–5 mm wide. Nectary green, unlobed, ca. 1 mm high. Filaments red, 8–10 mm and 6–8 mm long; anthers oblong, 3–3.5 mm long, ca. 1.5 mm wide, cream. Style red, villous for ca. ¾ its length from the base; stigma globose, ca. 2 mm wide, 1.5–1.8 mm wide, reddish. Berry oblong, tetragonous, green before maturity, ca. 15 mm long, ca. 6 mm thick; mature fruits not seen.

Distribution: Southern Ecuador. Known only from the Nudo de Sabanilla area near the border of Loja and Zamora-Chinchipe Provinces, ca. 2,800 m (Fig. 60).

Specimens examined: ECUADOR, LOJA: road from Yangana to Nudo de Sabanilla, S of Yangana, 1 km below top of ridge, Escobar 1547 (MO), 1547-A (MO).

This is one of several localized, endemic species in southern Ecuador, including *Fuchsia steyermarkii* and *F. lehmannii*. It is characterized by its dark, metallic-colored, narrowly elliptic-lanceolate leaves, purplish stems, and long, axillary flowers with narrow petals. These characters place it closest to the *F. venusta* species group, and it is probably closely related to *F. llewelynii* of northern Peru. Sandeman s.n. (K; Aug. 1938) from Almirante, Dept. Amazonas in northern Peru possibly belongs in this species. It is somewhat less pubescent than the Ecuadorian plants, with less markedly angled ovaries and shorter pedicels, but agrees well in other floral and foliar characters with this species. Nearly mature fruits are present in this collection; the berries are ellipsoid, 13 mm long, and 7 mm thick. The seeds measure ca. 1.5 mm long and ca. 1 mm wide.

33. **Fuchsia confertifolia** Fielding & Gardner, Sert. Pl. pl. 28. 1844. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):550. 1941. Munz, Proc. Calif. Acad. Sci.

IV. 25:42, *pl.* 6, *fig.* 30. 1943. TYPE: Peru, Dept. Amazonas, Bagasán (on path from Molinopampa to Moyobamba), 1830–1841, *Andrew Mathews 1478* (OXF, holotype; photograph, MO; K, isotypes).

Fuchsia dolichantha K. Krause, *Repert, Spec. Nov. Regni Veg.* 1:172. 1905. TYPE: Peru, Dept. Amazonas, Tambo Ventilla, E of Chachapoyas, 2,400–2,600 m, 1904–1921, *August Weberbauer 4390* (B, holotype, destroyed in World War II; photograph, F).

Densely-branched shrubs 1–2.5 m tall. Branchlets terete, 1.5–3 mm thick, usually less than 15 cm long, conspicuously ferrugineous-hirsute; older branches with red brown bark exfoliating in slender strips. Leaves densely crowded on branchlets and upper portions of older stems with internodes mostly 2–5 mm long, 2–4 leaves per node, usually ternate, subcoriaceous, elliptic-ovate, rounded to acute at the base, acute at the apex, 8–12 mm long, 3–5 mm wide, glabrous on both sides except for scattered hairs 1.0–1.2 mm long on the basal portions of the midvein or along the margins; secondary veins 4–5 on either side of the midvein; margin remotely glandular-denticulate or slightly revolute. Petioles hirsute-villous, 1–2 mm long. Stipules dark, filiform, 2–3.5 mm long, ca. 0.3 mm wide, persistent, often connate and divergent to reflexed. Flowers mostly 2–8, drooping, grouped in uppermost axils at the branch tips. Pedicels hirsute, 9–15 mm long. Ovary oblong, 4–5 mm long, 1.5–2 mm thick, pilose, 8-sulcate. Floral tubes narrowly funnelform, 35–50 mm long, 2–4 mm wide and slightly bulbous at the base, narrowed to 1.5–3 mm wide above the nectary, gradually widened above until 7–10 mm wide at the rim, glabrous to sparsely pilose outside, pilose inside for most its length. Sepals narrowly lanceolate, acuminate, 13–18 mm long, 4–5 mm wide, with tips connate into a tip ca. 2 mm long in bud. Tube and sepals red. Petals red, narrowly triangular with long, tapered tips, 9–14 mm long, 2.5–3 mm wide, $\frac{1}{3}$ – $\frac{1}{4}$ shorter than the sepals. Nectary unlobed, ca. 1.5 mm high. Filaments red, 6–10 mm and 4–7 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide. Style red, densely pilose for most its length; stigma subobconic, 4-cleft at the apex, 2–3 mm long, ca. 2 mm wide, exserted 4–5 mm beyond the anthers. Berry ellipsoid-ovoid, ca. 10 mm long, 5–7 mm thick; seeds tan, 1.8–2.1 mm long, 1–1.2 mm wide.

Distribution: Northern Peru. Endemic to cloud forest near high ridges of the mountains east of the Río Utcubamba in Dept. Amazonas, 2,600–3,200 m (Fig. 60).

Specimens examined: PERU, AMAZONAS: between Jumbilla and San Carlos, Prov. Bongará, *Weberbauer 7153* (F, GH, POM); S side of Molinopampa-Diosán Pass, N of Molinopampa, *Wurdack 1605* (F, NY, RSA, UC, US, USM).

This species is very distinctive in its densely crowded, small, leathery leaves and rust-colored hirsute stems. Its affinities are unclear, but it is placed in the *F. venusta* species group because of the coriaceous leaves, long, subracemose flowers, and somewhat ridged, delicate petals. It occupies the same restricted area as *F. pilosa*, *F. llewelynii*, and *F. wurdackii*, yet it is probably not sympatric with any of these species since it occurs at higher elevations.

34. *Fuchsia denticulata* Ruiz & Pavón, *Fl. Peruv. Chil.* 3:97, *pl.* 325, *fig. b.* 1802. Macbr., *Field Mus. Nat. Hist., Bot. Ser.* 13(4):553. 1941. Munz, *Proc. Calif.*

Acad. Sci. IV. 25:23, *pl.* 2, *fig.* 9. 1943. TYPE: Peru, "Cenchín, in cultis," probably Dept. Lima, 1778–1788, *Hipólito Ruiz & José Pavón* (MA N° 11/86, lectotype, here designated; photograph, MO). In the protologue, the locality is given as "Huassa-huassi et Cheuchín." The first site is in Junín, and the second apparently corresponds to the "Cenchín" on the lectotype label. Figs. 19, 42.

Fuchsia serratifolia Ruiz & Pavón, Fl. Peruv. Chil. 3:86, *pl.* 325, *fig.* b. 1802. Hook., Bot. Mag. t. 4174. 1845. Planch., Fl. Serres Jard. Eur. 5: t. 447. 1849. Sweet, Ornam. Fl. Gard. 2: t. 88. 1854. Essig, Nat. Hort. Mag. 13:12, *photo.* 1934. TYPE: Peru, Dept. Huánuco, Muña, 1778–1788, *Hipólito Ruiz & José Pavón* (MA, lectotype, here designated; photograph, MO).

Fuchsia leptopoda K. Krause, Repert. Spec. Nov. Regni Veg. 1:171. 1905. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):555. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:24, *pl.* 2, *fig.* 10. 1943. TYPE: Peru, Dept. Junín, Prov. Tarma, between Palca and Huacapistana, 2200–2600 m, 1904–1921, *August Weberbauer* 1772 (B, holotype, destroyed in World War II; photographs, F, POM; G, isotype).

Fuchsia siphonata K. Krause, Repert. Spec. Nov. Regni Veg. 1:171. 1905. TYPE: Peru, Dept. Junín, Prov. Tarma, mountains E of Huacapistana, 1904–1921, *August Weberbauer* 2178 (B, holotype, destroyed in World War II; photograph, F).

Fuchsia tacsoniiflora K. Krause, Repert. Spec. Nov. Regni Veg. 1:172. 1905. TYPE: Peru, Dept. Lima, near railroad from Lima to La Oroya, along streams above San Mateo, 3200 m, 1904–1921, *August Weberbauer* 252 (B, holotype, destroyed in World War II; photograph, F).

Erect to scandent shrubs 1.5–4 m tall or climbing in trees to 10 m above ground. Young growth subcanescent or occasionally pilosulous; branchlets terete, subdivaricate, green to wine red; older branches 5–20 mm thick with tan, exfoliating bark. Leaves 3–5-verticillate, mostly ternate or quaternate, rarely opposite, firmly membranous, (narrowly) elliptic to oblanceolate, acute to narrowly cuneate at the base, acute to subacuminate at the apex, 4–17 cm long, 1.5–6.5 cm wide, dull to nitid dark green and glabrous above, pale green and subglabrous to strigose mostly along veins and margins below; secondary veins 7–17 on either side of the midvein, often reddish below; margin denticulate. Petioles glabrous to loosely strigose, (5–)8–20(–25) mm long. Stipules triangular, firm, often connate, 2–2.5 mm long, ca. 1.5 mm wide, deciduous. Flowers few to numerous, axillary and pendant, usually grouped toward branch tips. Pedicels stout, smooth, 1–1.5 mm thick, 18–45 mm long, suberect in bud, drooping at anthesis, generally green. Ovary narrowly oblong, terete, 10–13 mm long, 3–4.5 mm thick, generally glabrous, green. Floral tube subcylindric, firm, walls 1–1.5 mm thick, smooth, (28–)36–47 mm long, (3–)4–8 mm wide at the base, sometimes very slightly narrowed above the nectary, straight or slightly widened above until (5–)6–12 mm wide at the rim, glabrous to puberulent outside, densely villous inside above the nectary for 7–10 mm, glabrous above. Sepals lanceolate, acuminate, 17–26 mm long, 4–7 mm wide, forming a tapered point in bud, spreading to subdivergent at anthesis. Tube waxy light pink, lavender, or light red; sepals pink to light red with light green to whitish tips or margins, at times entirely whitish green. Petals orange to scarlet, usually drying purple streaked, lance-oblong to oblanceolate, obtuse to broadly acute at the apex, slightly undulate, 14–18 mm long, 4–6(–7) mm wide, suberect at anthesis. Nectary green, unlobed, 2.5–3 mm high, ca. 1.5 mm thick. Filaments pink to light red, 14–23 mm and 8–18 mm long; anthers oblong, 4–6 mm long, 2–3 mm wide, white. Style stout, pink to light red, glabrous; stigma subclavate, subentire (very slightly 4-cleft at the apex), 3–4 mm long, 2–3.5 mm wide, dull white, exserted 2–12 mm beyond the anthers. Berry ellipsoid,

20–26 mm long, 10–12 mm thick, nitid green to red purple, smooth surfaced; seeds tan, 1.8–2.2 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Peru and Bolivia. Known from three main areas: the Pacific slopes of the Cordillera Occidental of Peru in Lima and Ancash, near springs and in moist canyons, 2,800–3,500 m; on the eastern slopes of the Peruvian Andes from Huánuco to Cuzco, in cloud forest and moist upland shrub vegetation, 2,500–3,400 m; and on the northeastern slopes of the Bolivian Andes in Depts. La Paz and Cochabamba, in cloud forest, 2,200–3,100 m (Fig. 61).

Representative specimens examined: PERU, ANCASH: Racrán, near Chiquián, *Ferreyra* 6208 (MO, US); Chiquián, *Ferreyra* 7435 (F, MO, RSA, US); Km 23, Caraz, Prov. Huaylas, *López-Guillén* 1904 (RSA); Caraz to Laguna de Parón, *López et al.* 8348 (MO); above Monterrey, 3 km below Huaraz, *Pennell* 15305 (PH). AYACUCHO: 41–47 km E of Tambo on road to Ayna, *Berry* 3050 (MO, USM), 3052 (MO, USM); above Yuraccyacu on Capprichio-Puncu trail, ca. 40 km NE of Tambo, *Madison* 10319-70 (MO, US, USM); above Jano, from Tambo to Ayna, *Plowman & Davis* 4678 (GH, K); Yanamonte, between Tambo and Río Apurímac, *Weberbauer* 5641 (F, GH, US); Choimacota valley, *Weberbauer* 7587 (F, G, GH, S), 7587a (F). CUZCO: Km 156–165 of Cuzco-Quillabamba road, Prov. La Convención, *Berry* 2573 (CUZ, MO), *Berry & Aronson* 3042 (MO, USM), 3043 (MO), 3048 (MO); Lucumayo valley, *Cook & Gilbert* 1356 (US); Yuncaipata, Santa Rita, Prov. Convención, *Vargas* 2656 (CUZ, MO); heights of Pintobamba, *Vargas* 3551 (CUZ); Quellomayo-Lucumayo, *Vargas* 4480 (BN, CUZ); Chawares, Prov. Convención, *Vargas* 20237 (CUZ); above Alfamayo, *Vargas* 22778 (MO). HUANCABELICA: Salcabamba, Prov. Tayacaja, *Stork & Horton* 10261 (F, UC); Montepungo, 5 km E of Surcubamba, Prov. Tayacaja, *Stork & Horton* 10367 (F, G, NA, UC). HUÁNUCO: Carpish, *Ferreyra* 1218 (MO, USM), 1730 (USM), 1832 (USM), 2088 (F, MO, NY, US, USM), 2387 (MO, US, USM); Mitobamba, above Mito, *Ferreyra* 6683 (MO, US, USM); Carpish, above Acomayo, *Hutchison et al.* 5921 (F, MO, NY, RSA, UC, US, USM); between Huánuco and Pampayacu, *Kanehira* 236 (GH); Km 29–35 NW of Hacienda Mitobamba, Huánuco-La Unión road, *Luteyn & Lebrón-Luteyn* 5501 (MO, NY); Muña, trail to Tambo de Vaca, *Macbride* 4284 (F, GH, US); Mito, *Macbride & Featherstone* 1403 (F, G, GH, US); ca. 23 km SE of Huánuco, *Macbride & Featherstone* 2082 (F, GH, US); Muña, *Pearce* 141 (K); Pillao, *Ruiz & Pavón* 11/85 (F); Pampayacu, *Sawada* P.8 (F); Pillao, *Woytkowski* 34163a (F, UC); Saraypampa, *Woytkowski* 34194 (F, MO, UC). JUNÍN: 4 km W of Comas, road Concepción-Satipo, *Berry & Aronson* 3065 (MO, USM); Comas, *Berry & Aronson* 3066 (MO, USM); 69 km above and W of Satipo on road to Concepción, *Berry & Aronson* 3072 (MO, USM); 62 km W of Satipo to Concepción, *Berry & Aronson* 3076 (MO, USM); Palca, near Tarma, *Ferreyra* 18738 (USM); Chilifruta, *Maguire & Maguire* 61646 (NY); Pangoa, *Mathews* 1168 (K); above Huacapistana, *Sandeman* 4508 (K, OXF); Chaca, 5 km from Comas, *Vargas* 22045 (CUZ). LIMA: Mani, near Huascay, *Acleto* 30 (MO, USM); between Infiernillo and Río Blanco, *Asplund* 10846 (S, US); Llacshishi, Prov. Huarochiri, *Ferreyra* 682 (MO, USM); near Palacala, above Surco, *Ferreyra* 3415 (MICH, MO, US); between Huascay and Cormo, *Ferreyra* 18392 (MO); Infiernillo, *Goodspeed et al.* 11549 (G, GH, NA, UC); Quebrada de San Mateo, *Isern* 2546 (F); San Mateo, 1 km E of city, *Hutchison* 669 (GH, UC, US, USM); Río Blanco, *Macbride & Featherstone* 723 (F, GH); Huamatanga, *Mathews* 541 (CGE, K, OXF); San Buenaventura, *Née s.n.* (MA 183589); Cerros de Matucana, *Raimondi* 188 (USM). PASCO: Vitoc, *Martinet* 1409 (P). WITHOUT LOCALITY: *Ruiz & Pavón s.n.* (BM, CGE, F, G, MA, MO). BOLIVIA, COCHABAMBA: ca. 42 km from Cochabamba to Chapare, *Berry* 2584 (MO), 2585 (MO), 2586 (MO); near Chulumani on way to Yungas de Tablas, *Cárdenas* 4087 (F, GH, RSA); Plumerito, to Río Tablas, *Cárdenas* 6282 (US). LA PAZ: road to Chulumani, *Albert de Escobar* 1305 (TEX); Yungas, *Bang* 731 (F, GH, NY, PH, US); near Zongo, 32 km from crest of ridge, *Beck* 2172a (MO); Unduavi, *Brooke* 6588 (BM, F, G, NY, U), 6850 (BM); *Buchtein* 143 (F, G, GH, NY); Zongo valley, *Holliday* 2/11 (K); San Felipe, Sur Yungas, *Holway & Holway* 632 (US); Km 50 La Paz-Chulumani, *Kelley* 1064 (BM, UC); near Combaya, Prov. Larecaja, *Mandon* 623 (GH); Río Aceramarca, Cordillera Real, *Tate* 718 (NY).

This is the most common and widespread member of the *Fuchsia denticulata* species group, an alliance of thick-tubed, axillary-flowered species centered in the Central Andes. It is characterized by its firm, subcylindrical flowers with waxy pink or light red floral tubes and narrow, green-tipped sepals, and also by the terete, ellipsoid fruits, stout pedicels, purple drying petals, large anthers 4–6 mm long, and nearly unlobed, clavate stigma.

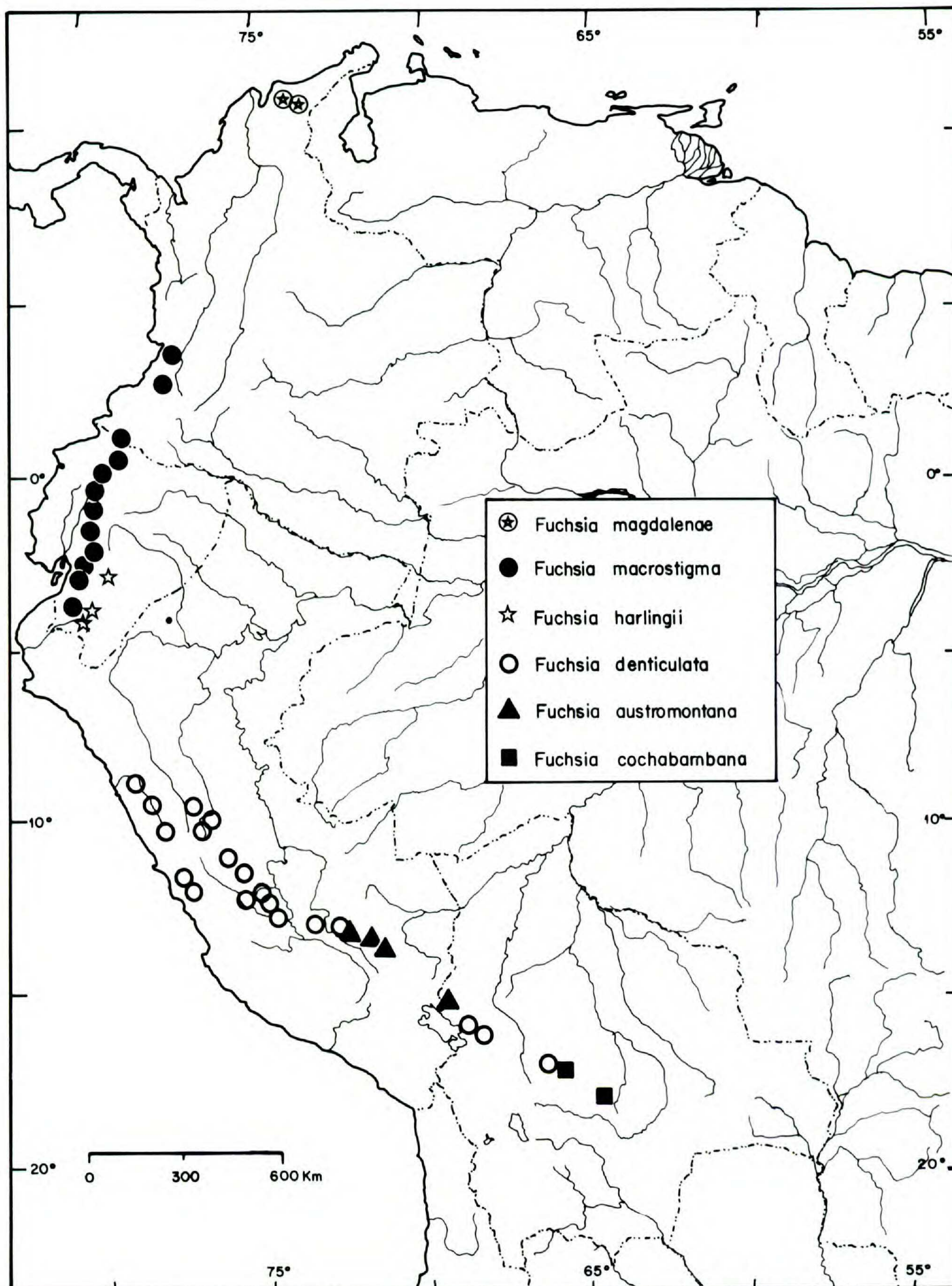


FIGURE 61. Distribution of the *Fuchsia denticulata* species group.

Fuchsia denticulata is the only member of the genus present on the dry Pacific slopes of the Cordillera Central in central Peru. It occurs there locally in isolated humid vegetation pockets, usually growing along streams, springs, or waterfalls. Plants from Ancash and Lima, such as the one used to describe *F. tacsoniiflora*,

TABLE 12. Comparison of diagnostic morphological characters of *Fuchsia denticulata*, *F. austromontana*, and intermediate Paucartambo collections.¹

	<i>F. denticulata</i>	Paucartambo Collections ¹	<i>F. austromontana</i>
Leaf length	4–17 cm	5–13 cm	2.5–8 cm
Petiole length	(5–)8–20(–25) mm	7–12 mm	3–12 mm
Floral tube texture	Smooth	Tuberculate	Subtuberculate
Floral tube color	Pink to light red	Dark red	Dark red
Difference between widest and narrowest part of tube	2–3 mm	5–6 mm	4–6 mm
Sepal angle at anthesis	Spreading	Spreading-recurved	Spreading-divergent
Stigma color	Cream	Red pink	Red
Fruit transection	Terete	Terete (?)	Quadrangular

¹ See text for list of specimens.

generally appear more robust, with thicker stems than plants of this species growing on the eastern slopes of the Andes. This is probably due, however, to their upright, shrubby habit in the sparse vegetation of the Pacific slopes, compared to the typically scandent habit of *F. denticulata* in the dense thickets of cloud forests on the eastern slopes. This east-west disjunction of *F. denticulata* in the Peruvian Andes is discussed in greater detail on p. 26.

Plants with narrow leaves and floral tubes like the type of *F. leptopoda* appear sporadically throughout Junín and Ayacucho, but they intergrade completely with more typical populations and maintain characteristic traits of *F. denticulata* such as green sepal tips and purple-streaked petals when dry. In cloud forests along the eastern slopes of the Andes, *Fuchsia denticulata* can be found as an erect shrub, a scandent shrub, or a high climbing vine. This wide variability in habit type accounts for most of the variability found in leaf size, pubescence, and floral dimensions, which Krause and Ruiz and Pavón, used to describe several of the taxa included in the above synonymy.

There is a gap of some 500 km between the nearest collections from Peru and Bolivia. The related *F. austromontana* occurs in the intervening areas in southernmost Peru, at higher elevations than would be expected for *F. denticulata*. Populations intermediate in some characters between these two species occur between 1,900 and 2,500 m along the road from Paucartambo to Pilcopata, near Buenos Aires, in Dept. Cuzco, Peru. These include the following collections: *Berry et al.* 2595 (MO, USM), 2598 (MO, USM; $n = 11$), 3007 (MO, USM); *Pennell* 13970 (F, PH), 14047 (PH); *Vargas* 10 (F); *Weberbauer* 6934 (F, GH, US); and *West* 7093 (GH, UC). These populations are sympatric with *F. tinctoria*, *F. vargasiana*, and *F. tuberosa* (sect. *Hemsleyella*), but occur several hundred meters lower than nearby populations of *F. austromontana* (Fig. 11). A comparison of these plants with *F. denticulata* and *F. austromontana* is presented in Table 12, showing their combination of distinctive and intermediate traits. Munz (1943) included some of the above specimens in *F. austromontana*; considering their ecological and morphological differences, however, this overextends the limits of that species. Further exploration in southern Peru (especially Dept. Puno) is needed to determine how widespread these variants are and if *F. denticulata* occurs in that area.

Fuchsia denticulata occurs sympatrically with *F. abrupta*, *F. corymbiflora*, *F. decussata*, *F. ferreyrae*, and *F. sanctae-rosae*. A Bolivian collection, *Beck 1266* (MO), is a probable hybrid with *F. sanctae-rosae* and is discussed under that species.

35. *Fuchsia austromontana* I. M. Johnston, J. Arnold Arbor. 20:242. 1939. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):548. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:22, pl. 1, fig. 8. 1943. TYPE: Peru, Dept. Cuzco, Prov. Paucartambo, between Pillahuata and Acanacu, 2,800 m, 26 July 1936, *James West 7083* (UC, holotype; photographs, NY, POM; GH, isotype).

Erect to occasionally climbing shrub 2–4 m tall. Young growth subcanescent to whitish pilose; branchlets subglabrous to puberulent, purplish, older branches with tan-brown, splitting bark. Leaves 3–5-verticillate, firmly membranous, acute to obtuse at the base, mostly acuminate at the apex, 2.5–8 cm long, 1–3 cm wide, dark green and subglabrous above, pale green and pubescent below, hairs usually denser along the midvein; secondary veins 5–9 on either side of the midvein; margin subentire to denticulate and sometimes slightly revolute. Petioles 3–12 mm long, reddish, densely pilose to lightly pubescent. Stipules linear-lanceolate, 2–4 mm long, 0.5–1 mm wide, subpersistent. Flowers generally few and pendant from upper leaf axils. Pedicels usually tuberculate, red, 14–35(–55) mm long. Ovary tetragonous, 6–8 mm long, 1.5–2 mm thick. Floral tube narrowly funnel-form, walls ca. 1 mm thick, (25–)34–50 mm long, 4–6 mm wide at the base, then narrowed to 2–5 mm wide for lower $\frac{1}{3}$, widened above until 10–12 mm wide at the rim, often $\pm$ verrucose, glabrous to densely pilose outside, (densely) villous inside in lower $\frac{1}{3}$ – $\frac{1}{4}$. Sepals lanceolate, acute to acuminate, thick-spongy, ca. 1.5 mm thick when fresh, often verrucose, 15–20 mm long, 5–7 mm wide, spreading to divergent at anthesis. Tube and sepals scarlet, the tips sometimes dull purple green. Petals deep red, usually drying a uniform purple, elliptic-obovate to suborbicular, 12–17 mm long, (7–)8–13 mm wide, rounded to broadly acute at the apex, spreading at anthesis. Nectary deeply 4-lobed to unlobed, ca. 2 mm high. Filaments red, 10–14 mm and 7–10 mm long; anthers oblong, 3.5–4.5 mm long, 2–3 mm wide, white. Style red, glabrous or with a few hairs; stigma subglobose, 4-cleft at the apex, 2–2.5 mm long, ca. 3 mm wide, red pink, exserted 1–10 mm beyond the anthers. Berry ellipsoid, reddish, tetragonous before maturity, 16–18 mm long, 8–11 mm thick; seeds tan, 1.4–1.7 mm long, 0.8–1.1 mm wide. Gametic chromosome number $n = 11$.

Distribution: From southern Cuzco Dept. in Peru to just beyond the Bolivian border in Dept. La Paz, Bolivia; upper cloud forest shrubs, 2,600–3,500 m (Fig. 61).

Representative specimens examined: PERU, CUZCO: Acanaco, *Balls B6708* (BM, K, UC, US); Km 145 of Cuzco-Quillabamba road, *Berry 2568* (CUZ, MO); 3035 (MO, USM); 8 km E of Acanaco Pass, Km 101 of Cuzco-Pilcopata road, *Berry et al. 2594* (MO, USM); between town of Marcapata and the baños termales, *Berry & Aronson 3025* (MO, USM); Km 143–152 of Ollantaytambo-Alfamayo road, 58–67 km NW of Ollantaytambo, *Luteyn & Lebrón-Luteyn 6451* (MO); region of Acanacu and Cordillera de Tres Cruces, *Luteyn & Lebrón-Luteyn 6372* (NY); Pillahuata, Cerro de Cusilluyoc, *Pennell 14110* (F, GH, PH, US); Km 144 from Ollantaytambo to Chaullay, *Plowman & Davis 4749* (GH, K); Huailai, Marcapata, *Vargas 1351* (BH, MO); between Achirani and Medias-Mayu, Prov. Paucartam-

bo, Dtto. Marcachea, Vargas 11121 (F, UC). BOLIVIA, LA PAZ: Italaque, Prov. Camacho, Cárdenas 3846 (LIL, POM).

This species is closely allied to *Fuchsia denticulata*, in a group of species with large, axillary flowers and thick floral tubes. *Fuchsia austromontana* grows at higher elevations than *F. denticulata* and has rounder, wider petals, tetragonous ovaries, and darker, somewhat verrucose flowers.

Fuchsia austromontana has a restricted range in southern Peru and just over the border into Bolivia. Populations that seem to intergrade with *F. denticulata* at intermediate elevations occur in Prov. Paucartambo, Dept. Cuzco, and are discussed under *F. denticulata* (Table 12 and Fig. 11). Another variant is Metcalf 30548 (A, BH, F, G, MO, UC, US; Peru, Dept. Puno, Prov. Sandia, 9 km from Limbano at Chamacani, 2,700 m); it resembles *F. austromontana* except for its more acute, narrower petals (15 mm long, 6–7 mm wide), strongly spreading sepal tips, elongate ovaries, and dense pubescence. More collections of the *F. denticulata* species group are needed from southern Peru to better evaluate the pattern of variability in the species that occur there.

- 36. *Fuchsia harlingii* Munz**, Aliso 7:409. 1972; Opera Bot., Ser. B, 3:16. 1974. TYPE: Ecuador, Prov. Loja, 14 km S of Saraguro, 3,000 m, 1–3 Aug. 1959, Gunnar Harling 6192 (S, holotype; photograph, MO). Fig. 25.

Fuchsia fosbergii Munz, Aliso 7:409. 1972; Opera Bot., Ser. B, 3:15. 1974. TYPE: Ecuador, Prov. Loja, Cruz Loma, Cerro Villonaco, 6 km W of Loja, 2,980 m, 14 Feb. 1945, Francis R. Fosberg & M. A. Giler 23036 (RSA 83773, holotype; US, isotype).

Erect to scandent shrubs 1–3 m tall. Branchlets subterete, 2–4 mm thick, glabrous or rarely strigose-villous; older branches with lustrous, purple brown bark, exfoliating in wide strips with age. Leaves opposite or ternate, firmly membranous to subcoriaceous, narrowly elliptic to elliptic-ovate, acute to rounded at the base, acute to acuminate at the apex, 3–7 mm long, 1.5–2.5 cm wide, glabrous and subnitid dark green above, pale green and glabrous to strigose-villous below; secondary veins 4–6(–7) on either side of the midvein, sometimes reddish below; margin glandular-serrulate. Petioles 3–6(–10) mm long. Stipules lance-deltoid, thick at the base, sometimes connate or recurved, 1–2 mm long, ca. 1.5 mm wide, subpersistent. Flowers few, pendant, and solitary in the upper leaf axils. Pedicels stout, 1–2 mm thick, 10–15 mm long. Ovary tetragonous, 6–7 mm long, 3–6 mm thick. Floral tube cylindric to narrowly funnelform, the base much wider than the ovary, (35–)44–53 mm long, very firm, 2–3 mm thick when fresh, (3–)4–9 mm wide at the base, 7–12 mm wide at the rim, gradually widened from the base to the rim or more often with subparallel sides, glabrous to villous outside, villous inside in lower ½. Sepals lance-oblong, 13–17(–21) mm long, 5–8 mm wide, 2–2.5 mm thick when fresh, spreading at anthesis, the tip blunt or less often acute in bud. Tube and sepals pale red to orange. Petals red, darker than the sepals, broadly elliptic-ovate, obtuse at the apex, 10–15 mm long, 7–11 mm wide, suberect at anthesis. Nectary shallowly 4–8-lobed, 1–2 mm high. Filaments red, 11–14 mm and 7–10 mm long; anthers oblong, 3–5 mm long, ca. 2 mm wide, cream. Style densely villous from the base to near the rim of the tube; stigma capitate, 4-cleft apically, 3–5 mm long, 3–5 mm wide, red. Mature berry not seen.

Distribution: Southern Ecuador, rare in cloud forest of Loja and Azuay Provinces, 2,600–3,300 m (Fig. 61).

Specimens examined: ECUADOR. AZUAY: Páramo and subpáramo N and NW of Páramo de Castillo, 6–8 km NNE of Sevilla de Oro, *Camp E-5184* (NY). LOJA: 10–12 km S of Saraguro, *Berry & Escobar 3193* (MO, QCA), *3195* (MO), *3206* (MO), *3207* (MO); Nudo de Guagrauma, S of Saraguro, *Correll E415* (LL); road from Loja to Saraguro, *Dodson & Thien 587* (DS); Cerro Arcana, *Espinosa & Williams 2490* (RSA); Km 51 on Panamerican Highway N of Loja, *Holm-Nielsen et al. 4701* (AAU, S); Saraguro, *Humboldt & Bonpland s.n.* (P); 12 km S of Saraguro, *King & Almeda 7840* (MO); Chuquirbamba, *Poortman 445* (P). SANTIAGO-MORONA OR ZAMORA-CHINCHIPE: between Loma de Galapagos and headwaters of Rio Tintas, *Steyermark 53462* (NY). WITHOUT LOCALITY: *Lobb s.n.* (K).

This is a member of the thick-tubed, axillary-flowered *Fuchsia denticulata* species group and is distinctive in its firm, short petiolate, few-veined leaves, the short pedicels, and the smooth, purplish stems. Collections from the type locality near Saraguro, Loja, are usually glabrous with cylindric flowers that are broad at the base and blunt-tipped. Plants from other localities, however, have flowers narrower at the base with narrowly funnelform floral tubes and acute tips. This difference in tube shape was used by Munz (1972) to describe *F. fosbergii*; at that time Munz had seen only one other sheet of *F. harlingii*. *Berry & Escobar 3194* (MO), from near Saraguro, is densely hirsute, yet was collected from a population of totally glabrous plants. *Camp E-5184* (NY), the northernmost collection from Azuay, is also unusual in its strigose-villous pubescence.

Fuchsia harlingii is sympatric with the more widespread *F. loxensis*, but no hybrids between the two were detected.

37. *Fuchsia cochabambana* P. Berry, sp. nov. TYPE: Bolivia, Dept. Cochabamba, Prov. Chapare, Km 104 of Cochabamba-Villa Tunari road, 3,100 m, 18 Dec. 1966, *Roy F. Steinbach 632* (US 2533496, holotype; F, LAM, MO, NY, U, isotypes).

Frutex 0.5–1.5 m altus, ramulis foliisque glabris vel puberulentis. Folia ternata vel interdum quaterna, subsessilia, elliptica vel anguste elliptico-lanceolata, basi acuta vel obtusa, apice acuminata, 3–12 cm longa, 1–5 cm lata, nervis secundariis utroque latere 11–14, margine valde denticulata vel serrulata; petiolis 1–3 mm longis; stipulis subpersistentibus, triangularibus, 2–3 mm longis, ca. 2 mm latis. Flores aurantiacorubri vel vivide coccinei, dependentes vel nutantes, axillares vel subracemosi ad apicem ramorum congesti; pedicellis 7–30 mm longis; ovario oblongo, 5–7 mm longo. Tubi florales anguste infundibuliformes, 45–58 mm longi, basi ca. 3 mm lati, superne sensim dilatati summo 7–10 mm lati. Sepala lanceolata acuminata 16–18 mm longa, ca. 5 mm lata. Petala rubra, in sicco saepe purpurascens, elliptica, 10–13 mm longa, 5–8 mm lata, apice obtusa vel late acuta. Filamenta antiseptala ca. 10 mm longa, antipetala 6–7 mm longa; antheris oblongis, ca. 3 mm longis, ca. 2 mm latis. Stylus ruber glaberque, stigmatibus rubro globosis apice leviter 4-fidis, ca. 3 mm longo, ca. 2 mm lato. Bacca matura non visa.

Shrubs 0.5–1.5 m tall. Young growth subglabrous to puberulent. Leaves ternate or less often quaternate, subsessile, firmly membranous, mostly elliptic or narrowly elliptic-lanceolate, acute to obtuse at the base, (sub-)acuminate at the apex, 3–12 cm long, 1–5 cm wide, subglabrous above, subglabrous to usually puberulent along the veins below and usually purple-flushed; secondary veins 11–14 on either side of the midvein; margin conspicuously dentate or serrate. Petioles 1–3 mm long. Stipules triangular, membranous when young to thick and recurved when old, 2–3 mm long, ca. 2 mm wide, subpersistent. Flowers pendant, few to numerous, axillary or subracemose, but always tightly grouped at the

branch tips. Pedicels 7–30 mm long. Ovary oblong, 5–7 mm long, ca. 2 mm thick. Floral tubes narrowly funnelform, 45–58 mm long, ca. 3 mm wide and slightly bulbous at the base, narrowed to ca. 2 mm wide above the nectary and gradually widened above until 7–10 mm wide at the rim, subglabrous to pubescent outside, pilose inside in lower ½. Sepals lanceolate, acuminate, 16–18 mm long, ca. 5 mm wide, with a narrow tip 2.5–3.5 mm long in bud. Tube and sepals orange red to bright crimson. Petals red, often drying purplish, elliptic, 10–13 mm long, 5–8 mm wide, obtuse to broadly acute at the apex. Nectary unlobed, ca. 2 mm high. Filaments light red, ca. 10 mm and 6–7 mm long; anthers oblong, ca. 3 mm long, ca. 2 mm wide. Style red, glabrous; stigma globose, 4-cleft apically, 2–3 mm long, ca. 2 mm wide, reddish. Mature berry not seen.

Distribution: Bolivia, scattered to locally frequent cloud forest shrubs in Depts. Cochabamba and Santa Cruz, 2,500–3,100 m (Fig. 61).

Specimens examined: BOLIVIA, COCHABAMBA: Cochabamba-Villa Tunari road, *Badcock* 711 (K); Corani, *Cárdenas* 5754 (K, US); Siberia, *Cárdenas* 5764 (US). SANTA CRUZ: 24 km W of Comarapa on Carretera Fundamental 4, *Davidson* 3851 (MO); Fortaleza, between Siberia and Comarapa, *Vogel* 499 (U).

This species is included in the *Fuchsia denticulata* species group because of its long, firm floral tubes and purple drying petals. It differs from other members of this group in its funnelform floral tubes, nearly sessile, serrulate leaves, and flowers tightly grouped at the branch tips. This is one of only two species of sect. *Fuchsia* endemic to Bolivia, where it probably occurs sympatrically with *F. sanctae-rosae*.

38. *Fuchsia macrostigma* Benth. *Pl. Hartw.* 129. 1844. *Fuchsia macrostigma* var. *typica* Munz, *Proc. Calif. Acad. Sci.* IV. 25:31, *pl.* 3, *fig.* 17. 1943. Based on *F. macrostigma* Benth. *Fuchsia macrostigma* var. *macrostigma*, Munz, *Opera Bot.*, Ser. B, 3:19. 1974. TYPE: Ecuador, Prov. El Oro, in mountains of Paccha, 1841–1843, *Theodor Hartweg* (K, holotype; photograph, MO).

Fuchsia longiflora Benth. *Pl. Hartw.* 177. 1845. *Fuchsia macrostigma* var. *longiflora* (Benth.) Munz, *Proc. Calif. Acad. Sci.* IV. 25:31. 1943; *Opera Bot.*, Ser. B, 3:20. 1974. TYPE: Ecuador, Prov. Pichincha, W side of Volcán Pichincha, between Quito and Nanegal, 1841–1843, *Theodor Hartweg* (K, holotype).

Fuchsia spectabilis Hooker ex Lindley, *Gard. Chron.* 1848:319, *t.* May 13, 1848. Hook., *Bot. Mag.* 74: *t.* 4375. June 1, 1848. Lem., *Fl. Serres Jard. Eur.* 4:360, *t.* 1848. Paxt., *Paxton's Mag. Bot.* 16:255, *t.* 1849. Ysabeau, *Journ. Hort. Prat. Belg.* 7:225, *t.* 1849. Fancourt, *Gard. Chron.* 1850:71, *fig.* 1850. TYPE: cultivated in London, England, by the Veitch nurseries, 1848, from seeds collected by William Lobb in the mountains of Cuenca, Prov. Azuay, Ecuador, *William J. Hooker* (K, holotype).

Fuchsia macrostigma var. *pubens* I. M. Johnston, *Contr. Gray Herb.* 75:34. 1925. TYPE: Ecuador, Prov. Chimborazo, vicinity of Huigra, mostly on the Hacienda de Licay, 3 Sept. 1918, *Joseph N. Rose & George M. Rose* 22479 (US 1022130, holotype; photographs, POM, UC; GH, NY, isotypes).

Erect shrubs 0.5–1.5 m tall. Branchlets stout, subsucculent, 2–7 mm thick, terete or angled, green to dull purple; older branches 8–15 mm thick, dull tan, with finely fissured bark. Leaves opposite or less often ternate, firmly membranous, narrowly to broadly elliptic to (ob-)ovate, acute at the base, acute to acuminate at the apex, 6–27 cm long, 3–12 cm wide, velvety dark green and subglabrous to puberulent above, pale green to wine purple below with strigose to

villous pubescence mostly along the veins; secondary veins 9–15(–22) on either side of the midvein; margin remotely denticulate with small, glandular teeth. Petioles stout, 2–3 mm thick, 15–30(–35) mm long, strigose, green to purple. Stipules dark, triangular, sometimes connate, 2–2.5 mm long, ca. 2 mm wide, deciduous. Flowers few and axillary in upper nodes. Pedicels stout, 2–2.5 mm thick, 8–20(–30) mm long, pubescent, spreading to ascending. Ovary cylindrical, 8–12 mm long, 3–5 mm thick, green, verrucose, 4–8 sulcate. Floral tubes narrowly funnelform, 50–80 mm long, 2–5 mm wide and bulbous at the base, gradually widened above until 4–10 mm wide at the rim, subglabrous to villous outside, sparsely pilose inside in lower $\frac{1}{2}$; tube firm-spongy, 1–1.5 mm thick when fresh, often curved downward in distal $\frac{1}{2}$. Sepals lance-oblong, 14–23 mm long, 7–8 mm wide, thick-spongy, 1–2 mm thick when fresh, apiculate, divergent, tips free and spreading in bud. Tube pale to dark red; sepals red with dull green tips. Petals bright red, shorter than the sepals, orbicular to broadly obovate, 12–18 mm long, 10–19 mm wide, undulate, rounded at the apex, strongly spreading. Nectary green, unlobed, ca. 3 mm high and ca. 1.5 mm thick. Filaments red, 8–12 mm and 5–8 mm long; anthers oblong, 2.5–3.5 mm long, ca. 1.5 mm wide. Style pink, sparsely pubescent to subglabrous; stigma massive, tetragonous, 3–5 mm long, 4–6 mm wide, with 4 mound-like, sticky lobes, cream to pink. Berry ellipsoid, 8-sulcate until fully ripe, verrucose, 20–22 mm long, 8–12 mm thick; seeds tan brown, 2–2.5 mm long, 1.2–1.6 mm wide.

Distribution: Cordillera Occidental of Colombia and Ecuador, infrequent in moist cloud forest thickets on Pacific slopes, 1,000–2,500 m (Fig. 61).

Representative specimens examined: COLOMBIA, CAUCA: Km 42–47 NE of Uribe, *Luteyn & Lebrón-Luteyn* 7418 (COL, NY). NARIÑO: between Río Miraflores and Río San Martín, Volcán Cumbal region, *Ewan* 16165 (POM, US); trail from Mayasquer to Tambo, *Vogel* 284 (U). VALLE: above Querebral, Las Colonias, *Cuatrecasas* 23901 (F). ECUADOR, AZUAY: W of Patul, 3 km between Huahualcay and Río Patul, below Pasas de Pinglón, *Steyermark* 52613 (NY). BOLIVAR: Alto de Telimbela, *Acosta Solis* 7156 (F); Simiatug, Hacienda Talahua, *Penland & Summers* 614 (POM), 657 (F, POM). CAÑAR: N rim of valley of Río Cañar, *Camp E-2895* (NY, RSA). CARCHI: Km 50 Tulcán-Maldonado road, *Boeke* 861 (MO); Km 71 on Tulcán Maldonado road, *Holm-Nielsen et al.* 6011 (AAU); Los Olivos, *Mexia* 7462 (F, NA, UC, US). CHIMBORAZO: Sibambe, Hacienda La Carmela, *Acosta Solis* 5367 (F); 5 km from Huigra, Cañon del Río Chanchán, *Camp E-3376* (GH, MO, NY, P, RSA, UC, US); foot of Volcán Chimborazo, *Spruce in 1860* (K). COTOPAXI: 5 km above Pilaló, *Berry & Berry* 2549 (MO); 3 km E of Macuchi, Quevedo-Latacunga road, *Dodson & Gentry* 10152 (MO); Pilaló, *Holm-Nielsen & Jeppesen* 1549 (AAU, DS). EL ORO: between La Chorita and Portovelo, *Hitchcock* 21168 (GH, NY, US); along trail from Sambotambo, near highway to Portovelo, *Steyermark* 54221 (NY). IMBABURA: Cerro de Pinam, *Acosta Solis* 8505 (F); trail between Irubí and Apuela, N of Volcán Cotocachi, *Drew E-131* (RSA, US). PICHINCHA: valley of Río Pilatón, below Garretas, *Asplund* 9709 (S); above Río Toachi, *López-Palacios* 4224 (MERF, MO); Km 72–74 of old road Quito-Santo Domingo de los Colorados, *Luteyn & Lebrón-Luteyn* 5651 (NY); 13 km NW of Nono, road to Puerto Quito, *Luteyn et al.* 6520 (MO, NY); San Ignacio, Km 23 of Aloag-Santo Domingo road, *Sparre* 14583 (S); Km 37–50 along Río Saloya, between Volcán Atacaso and Volcán Pichincha, *Steyermark* 52543 (NY).

The flowers of this species are rather striking; they are long and narrow, usually horizontally disposed and recurved in the lower one half, with round, spreading petals, and a large, tetragonous stigma. Although it is a very distinctive species, it is placed in the *Fuchsia denticulata* species group because of its thick-tubed, axillary flowers, stout pedicels, and greenish sepal tips. The round petals, sulcate ovaries, and thick tubes also ally it to *F. ampliata*, however.

Fuchsia macrostigma is restricted to the Cordillera Occidental of the northern Andes and is the only species to be found in the southernmost remnant of cloud

forest in El Oro Province of southern Ecuador. Differences in floral tube length and degree of pubescence were used to describe the taxa listed in synonymy, but these characters vary too widely and continuously between populations to be of any taxonomic significance.

No naturally occurring hybrids of this species were found, but one of the earliest artificial hybrids in sect. *Fuchsia*, *F. dominiana* (van Houtte, 1854) was a cross between *F. macrostigma* and *F. denticulata*. *Fuchsia macrostigma* occurs sympatrically with *F. putumayensis*, *F. scabriuscula*, *F. sessilifolia*, and *F. sylvatica*.

- 39. *Fuchsia magdalenae*** Munz, Proc. Calif. Acad. Sci. IV. 25:25, pl. 2, fig. 5. 1943. TYPE: Colombia, Dept. Magdalena, above San Miguel, at edge of páramo, 3,000 m, July 1932, William E. Seifriz 392 (US 1572275, holotype; photographs, MO, NY, UC).

Fuchsia lampadaria J. O. Wright, Bot. Jour. Linn. Soc. 77:113, fig. 1978. TYPE: Cultivated in Reading, Great Britain in 1976, from seeds collected in Colombia, Dept. Magdalena, SE slopes of the Sierra Nevada de Santa Marta, Trombachuca Valley, uppermost forests, 3,300 m, 1975, by Michael Adams and George Bernard, J. O. Wright (RDG, holotype, not seen).

Shrubs 2–5 m tall. Young growth glabrous to lightly strigose; branchlets purplish, older branches red brown, with bark exfoliating in strips. Leaves ternate or less often quaternate, firmly membranous to subcoriaceous, (narrowly) elliptic to ovate, acute to rounded at the base, acute to subacuminate at the apex, 2.5–8.5(–12) cm long, 1–4(–6) cm wide, dark green and mostly glabrous above, pale green with purplish veins and glabrous below, except for hairs usually present along the margin; secondary veins 8–14 on either side of the midvein; margin denticulate or subentire. Petioles purplish, sparsely strigose, 4–25(–30) mm long. Stipules lanceolate to triangular, dark, ca. 1 mm long, deciduous. Flowers pendant and solitary in upper leaf axils. Pedicels firm, 15–60 mm long, mostly red. Ovary ovoid-ellipsoid, glabrous, 7–10(–11) mm long, 3–3.5 mm thick. Floral tube subcylindric, (35–)42–60 mm long, firm-fleshy, ca. 1 mm thick when fresh, 3.5–6 mm wide at the base, sometimes slightly narrowed above the nectary, very gradually widened above until 6–10 mm wide at the rim, glabrous inside and outside. Sepals lanceolate, acute to subacuminate, 13–18(–22) mm long, 4–5(–6) mm wide, blunt-tipped in bud, spreading at anthesis. Tube slightly purplish at the base and orange red above, sepals nitid orange red with greenish tips. Petals orange red, suborbicular to obovate or subrhomboid, sometimes with irregular margins, 11–19 mm long, 7–12(–18) mm wide, usually with a narrowly acute tip. Nectary an uneven band of lustrous tissue lining the basal 3–6 mm of the floral tube, without prominent lobes. Filaments light red, 12–16 mm and 8–13 mm long; anthers oblong, 3.5–4 mm long, ca. 2.5 mm wide, cream. Style light red to orange, glabrous; stigma capitate, lightly 4-cleft apically, 2–3 mm long, 2–4 mm wide, light red to orange, exserted 4–10 mm beyond the anthers. Berry ellipsoid, 20–24 mm long, 10–12 mm thick, usually dark purple; seeds (1.5–)2–2.5 mm long, 1–1.3 mm wide. Gametic chromosome number $n = 22$.

Distribution: Endemic to upper cloud forest of the Sierra Nevada de Santa Marta in northeastern Colombia; (2,000–)3,000–3,350 m (Fig. 61).

Representative specimens examined: COLOMBIA, MAGDALENA: SE slopes Sierra Nevada de Santa Marta, Dirincune Sabana, watershed of Río Donachui, *Cuatrecasas & Romero Castañeda* 24514 (COL, RSA, US); San Antonio, Sierra Nevada de Santa Marta, *Hanbury-Tracy* 504 (K), 518 (K); San Miguel, *Karsten s.n.* (W); Páramo in quebrada from Río Frío, ca. 10°55'N, 73°53'W, *Kirkbride & Forero* 1759 (COL, MO); from Páramo to Cebolleta, *Romero Castañeda* 7177 (COL); Pico Hacha-Sierra Nevada, *Schlim* 800 (BM, F, G, K, MPU, P); between Pueblo and San Miguel, *Seifriz* 537 (US).

This species is placed in the *Fuchsia denticulata* species group because of its thick-tubed, nearly cylindric, axillary flowers, but it is highly distinct from all other species in sect. *Fuchsia* in its non-annular, band type nectary, which resembles those found in sects. *Ellobium* and *Hemsleyella* (Figs. 45 and 48). Pubescence is completely lacking inside the tube and on the style, and the flowers have rounded petals that often have uneven margins. *Fuchsia magdalenae* is also tetraploid and has biporate pollen. The above assemblage of unusual characteristics suggests that this species may have been an early offshoot of the section that was isolated on an outlying portion of the Andes.

Fuchsia magdalenae is restricted to the upper cloud forest and subpáramo belt that more or less continuously surrounds the high peaks of the isolated Sierra Nevada de Santa Marta range. It is the only species of *Fuchsia* to occur there, although Wright (1978a) recently described *F. lampadaria* from this same area. Most of the differences he states for that species, however, are insignificant when all the specimens from the Santa Marta area are examined. The larger leaf dimension he describes may also be related to the controlled greenhouse conditions in which his plants were grown.

40. *Fuchsia simplicicaulis* Ruiz & Pavón, Fl. Peruv. Chil. 3:89. pl. 322, fig. a. 1802. Hook., Bot. Mag. t. 5096. 1859. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):563. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:41, pl. 5, fig. 29. 1943. Morley & Everard, Wild Flowers of the World, pl. 173, fig. C1. 1970. Travis, Fuchsia Annual 1975:21, photo. 1975. TYPE: Peru, Dept. Huánuco, woods at Muña, 1778–1788, *Hipólito Ruiz & José Pavón* (MA N° 11/92, lectotype, here designated; photograph, MO).

Scandent shrubs 2–5 m tall, sparsely verticillately branched, with ultimate branches pendulous. Branchlets subterete, puberulent, older stems with light red, exfoliating bark. Leaves ternate or quaternate, membranous, linear-lanceolate to ovate-lanceolate, acute to narrowly obtuse or truncate at the base, acuminate at the apex, 8–15 cm long, 1–3.5 cm wide, glabrous above, glabrous to scattered pilose below or along the margin; secondary veins 10–18 on either side of the midvein; margin subentire. Petioles glabrous to puberulent, 2–6 mm long. Stipules triangular, 1–2 mm long, ca. 0.9 mm wide, subpersistent. Flowers in simple to multiple, pendant, involucrate racemes, with flowers 3–4 per whorl and internodes 1.5–6 cm long; rachis 8–30 cm long; bracts thinly membranous, sessile, concave, ovate-lanceolate, broadly rounded and clasping the stem at the base, acuminate at the apex, 1–5 cm long, 0.5–1.5 cm wide. Pedicels puberulent, 5–10 mm long. Ovary oblong-ellipsoid, puberulent or velutinous, 5–6 mm long, 2–2.5 mm thick. Floral tube narrowly funnelform, 40–50 mm long, bulbous and 3–4 mm wide at the base, narrowed to 1.5–2 mm wide above the ovary, then gradually widened above until 5–7 mm wide at the rim, finely pilose outside, pilose inside.

Sepals lanceolate, puberulent on both sides, acuminate, 16–20 mm long, ca. 4 mm wide. Tube and sepals light reddish pink. Petals red, linear-lanceolate to elliptic, acute to narrowly acuminate at the apex, 9–13 mm long, 2–3(–5) mm wide. Nectary apparently unlobed, ca. 1.5 mm high. Filaments 10–12 mm and 7–8 mm long; anthers oblong, 3–4 mm long, ca. 2 mm wide. Style pilose from base up to the rim of the tube; stigma globose, 4-parted at the apex, 2.5–3.5 mm long, ca. 2 mm wide. Berry ellipsoid, puberulent, 11–13 mm long, ca. 8 mm thick; seeds tan, ca. 1.2 mm long, ca. 0.7 mm wide.

Distribution: Central Peru. Rare in cloud forests in Depts. Huánuco, Junín, and Pasco, eastern slopes of the Andes; 2,200–2,500 m (Fig. 62).

Specimens examined: PERU, HUÁNUCO: Muña, *Lobb 119* (K), *Macbride 4014* (BH, F, GH, K, S, US), *Pearce 133* (K). JUNÍN: Vitoc, *Martinet 1310* (P). PASCO: Oxapampa, *Soukup 1804* (GH, US, USM). WITHOUT LOCALITY: *Lobb s.n.* (K).

This is one of two very rare and unusual species with whorls or involucre of thin, membranous bracts and short-pedicelled flowers. The other species, *Fuchsia ceracea*, also occurs in Huánuco, but has much larger bracts and flowers, with shorter petals. Both species are glabrous except for the puberulent or velutinous young stems, pedicels, and flowers. Two other species from Central Peru, *F. coriacifolia* and *F. sanmartina*, seem to be derived from, or at least closely related to the above species. Their relationships are discussed further under the *F. simplicicaulis* species group (p. 54).

41. *Fuchsia ceracea* P. Berry, sp. nov. TYPE: Peru, Dept. Huánuco, Prov. Huánuco, in tree along stream, 5 km W of Carpish tunnel between Huánuco and Tingo María, 2,500 m, 4 Aug. 1978, *Paul E. Berry & James Aronson 3081* (MO 2720597, holotype; MO, USM, isotypes). Fig. 31.

Frutex scandens dependensque 3–6 m altus, praeter flores juvenes pedicellosque pilosos glaber. Folia opposita vel ternata, firme membranacea, lanceolata vel anguste ovata basi obtusa vel leviter auriculata aliquantum inaequalia, apice acuta, 8–15 cm longa, 4–6 cm lata, utrinque ceracea, nervis secundariis utroque latere 7–10, margine integerrima; petiolis leviter tortis 2–20 mm longis. Flores dependentes in verticillis involucratis 2–3 floralibus ad apicem ramorum dispositi; bracteis pruinosis, tenuiter membranaceis, concavis, sessilibus, late ovatis, 4–12 cm longis, 1.5–5 cm latis; pedicellis 7–15 mm longis; ovario ellipsoideo ca. 7 mm longo. Tubi florales vivide rosei vel lavandulacei, 9–13 cm longi, basi 6–7 mm lati inde 3–5 mm lati constricti superne gradatim dilatati summo 8–9 mm lati extus glabrati vel puberuli. Sepala lanceolata acuminata 28–30 mm longa 6–7 mm lata. Petala coccinea vel atropurpurea, ovata, late acuta, 5–7 mm longa, ca. 4 mm lata. Filamenta pallide rosea, antisepala 13–14 mm longa, antipetala 9–10 mm longa, antheris oblongis 4–5 mm longis ca. 3 mm latis. Stylus puberulus, stigmate magno subtetragono, 4-lobato, 4–5 mm longo ca. 4 mm lato. Bacca matura non visa. Numerus gameticus chromosomatum $n = 11$.

Climbing shrub or dangling liana in trees to 6 m above ground, the ultimate branches pendant. Plants glabrous except for puberulent young flowers and pedicels. Leaves opposite or ternate, firmly membranous, lanceolate to narrowly ovate, obtuse to unequal or slightly auriculate at the base, acuminate at the apex, 8–15 cm long, 4–6 cm wide, waxy green on both surfaces; secondary veins 7–10 on either side of the midvein; margin entire. Petioles reddish, slightly twisted, 2–20 mm long. Stipules narrowly triangular, 1.5–2 mm long, ca. 0.7 mm wide, subpersistent. Flowers in simple, pendant, involucre racemes, with 2–3 flowers per whorl and internodes 2–6 cm long; bracts thin membranous, concave, sessile,

pruinose, broadly ovate, acuminate at the apex, clasping the stem at the base, 4–12 cm long, 1.5–5 cm wide. Pedicels 7–15 mm long. Ovary ellipsoid, ca. 7 mm long, ca. 3 mm thick. Floral tube subcylindric to narrowly funnelform, (9–)10–13 cm long, bulbous and 6–7 mm wide at the base, narrowed to 3–5 mm wide above the nectary, slightly widened above until 8–9 mm wide at the rim, puberulent to subglabrous outside, pubescent inside in lower $\frac{1}{2}$. Sepals lanceolate, acuminate, 28–30 mm long, 6–7 mm wide, suberect at anthesis. Tube and sepals lavender to bright pink, tube white inside. Petals crimson to dark purple, ovate, broadly acute, 5–7 mm long, ca. 4 mm wide, suberect at anthesis. Nectary light green, unlobed, ca. 3 mm high. Filaments white pink, 13–14 mm and 9–10 mm long; anthers oblong, 4–5 mm long, ca. 3 mm wide. Style lavender pink, puberulent for most its length; stigma massive, subtetragonous, 4-lobed at the apex, 4–5 mm long, ca. 4 mm wide, light pink. Berry not seen. Gametic chromosome number $n = 11$.

Distribution: Very rare climbers in cloud forest, known just from Panao and the Carpish area of Dept. Huánuco, Peru; 2,500–2,850 m (Fig. 62).

Specimens examined: PERU, HUÁNUCO: above La Molina, near Panao, *Asplund 13699* (S); Carpish, *Asplund 14857* (RSA—a mixed collection with *F. corymbiflora*).

This species and *Fuchsia simplicicaulis* are the only two species in the genus with involucrate inflorescences and sessile concave bracts. *Fuchsia ceracea* has unusual waxy leaves, pruinose bracts, and very long floral tubes. The petals are less than one quarter as long as the sepals and are the proportionately most reduced of any species in sect. *Fuchsia*. It is extremely rare and is known only as a liana with long, unbranched, hanging stems. *Fuchsia abrupta* and *F. corymbiflora* both grow in the same area as *F. ceracea*, but they are lower shrubs and occur in more open thickets.

42. *Fuchsia coracifolia* P. Berry, sp. nov. TYPE: Peru, Dept. Pasco, Prov. Oxapampa, Huancabamba, 1863–1865, *Richard Pearce 565* (K, holotype; photograph, MO).

Frutex plerumque glaber 1–2 m altus. Folia coriacea subsessilia opposita vel ternata, basi rotundata vel subcordata apice acuta vel acuminata 3–6 cm longa 1–2.5 cm lata superne atroviridia subtus multo pallidioria, nervis strigulosis; nervis secundariis utroque latere 4–5 versus marginem gradatim inconspicuis; margine subdenticulata; petiolis 1–2 mm longis; stipulis plerumque connatis, subincrassatis, 2–3 mm longis, 2–3.5 mm latis, subpersistentibus. Flores rosei, numerosi et dependentes in racemo terminali et laxo dispositi, basi oppositi vel ternati apice gradatim alterni; rhachidi 3–9 cm longa; bracteis sessilibus anguste ovatis 10–20 mm longis 5–10 mm latis; pedicellis 5–15 mm longis; ovario oblongo 5–6 mm longo. Tubi florales firmi, anguste infundibuliformes, 52–58 mm longi, basi 3–3.5 mm lati et parum bulbosi inde 2.5–3 mm lati constricti superne gradatim dilatati summo 6–10 mm lati ubique plerumque glabrati. Sepala firma, ca. 1.5 mm crassa, oblongo-ovata, acuta, 17–19 mm longa 7–9 mm lata. Petala lanceolata acuta 10–12 mm longa ca. 4 mm lata. Filamenta antisepala 8–10 mm longa antipetala 6–7 mm longa, antheris oblongo-reniformibus 3–3.5 mm longis 2–2.5 mm latis. Stylus glaber, stigmati conico ca. 2 mm longo ca. 2.5 mm lato apice leviter 4-fisso. Bacca non visa.

Apparently simply branched low shrubs 1–2 m tall. Branchlets glabrous, slightly angled; older stems with whitish tan bark. Leaves opposite or ternate, firmly coriaceous, rounded to subcordate at the base, acute to acuminate at the apex, 3–6 cm long, 1–2.5 cm wide, dark green and strigillose along the veins above, much paler whitish green and strigillose along the red veins below; secondary

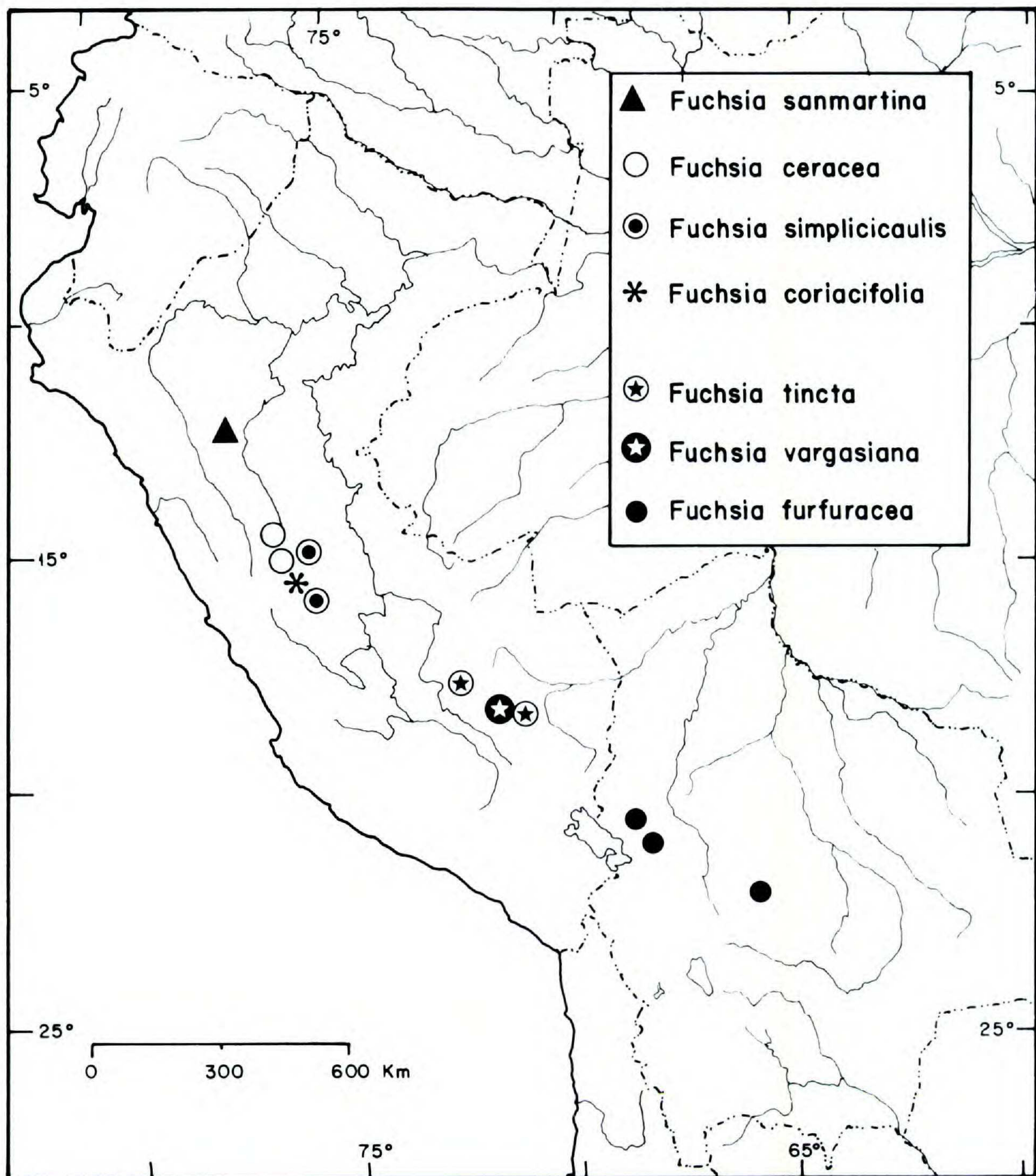


FIGURE 62. Distribution of the *Fuchsia simplicicaulis* and *F. tincta* species groups.

veins 4–5 on either side of the midvein, becoming inconspicuous towards the margin, the midvein prominent below; margin subdentate. Petioles 1–2 mm long, glabrous. Stipules mostly connate, firm, 2–3 mm long, 2–3.5 mm wide, subpersistent. Flowers numerous and pendant in loose, terminal racemes 3–9 cm long; bracts narrowly ovate, sessile, 10–20 mm long, 5–10 mm wide, opposite to ternate at the base and becoming alternate towards the end of the raceme. Pedicels 5–15 mm long, glabrous. Ovary ovoid, 5–6 mm long, ca. 3 mm thick. Floral tube narrowly funnelform, firm, 52–58 mm long, 3–3.5 mm wide and slightly bulbous at the base, narrowed to 2.5–3 mm above the nectary, then gradually widened above until 6–10 mm wide at the rim, mostly glabrous outside, glabrous inside. Sepals firm, ca. 1.5 mm thick, oblong-ovate, acute at the apex, 17–19 mm

long, 7–9 mm wide. Flowers rose. Petals lanceolate, acute at the apex, 11–12 mm long, ca. 4 mm wide. Nectary unlobed, 1.5–2 mm high. Filaments 8–10 mm and 6–7 mm long; anthers oblong-reniform, 3–3.5 mm long, 2–2.5 mm wide. Style glabrous; stigma conic, slightly 4-cleft at the apex, ca. 2 mm long, ca. 1.5 mm wide. Berry not seen.

Distribution: Known only from the type specimen, from central Peru, in Dept. Pasco near the Huánuco border (Fig. 62).

The ovate, sessile bracts, short pedicels, and inflorescence with opposite or ternate basal flowers place this species in the *Fuchsia simplicicaulis* species group. It is distinct from related species in having coriaceous, nearly sessile leaves and thick floral tubes. The inflorescence of *F. coriacifolia* seems to be derived from the involucrate type of *F. simplicicaulis* and *F. ceracea* and is transitional between these and the alternate-flowered, racemose inflorescences of the related *F. sanmartina*.

43. *Fuchsia sanmartina* P. Berry, sp. nov. TYPE: Peru, Dept. San Martín, Dist. Hualaga, Valley of Río Apisoncho, 30 km above Jucusbamba, 7°55'S, 77°10'W, 2,800 m, 6 Aug. 1965, A. C. Hamilton & P. M. Holligan 1065 (K, holotype; photograph, MO; NY, S, UC, isotypes).

Frutex scandens 1.5–10 m altus, ramulis foliisque junioribus puberulenti-velutinis. Folia plerumque ternata interdum opposita, firme membranacea, anguste elliptico-ovata, basi obtusa vel rotundata aliquantum inaequalia apice acuta vel acuminata, 5–15 cm longa, 1.5–6 cm lata, subtus nervis plerumque puberulentis; nervis secundariis utroque latere 9–11, margine subintegerrima vel denticulata; petiolis puberulentis 3–20 mm longis; stipulis anguste triangularibus, ca. 2 mm longis, deciduis. Flores numerosi et dependentes, vivide rubri, racemis terminalibus dispositi; rhachidi 7–16 cm longa; bracteis 8–50 mm longis, 5–25 mm latis, petiolis 1–8 mm longis; ovario 7–8 mm longo. Tubi florales subcylindrici 55–76 mm longi basi 3–4 mm lati et parum bulbosi, inde 2–3 mm lati constricti superne gradatim dilatati summo 6–8 mm lato extus puberuli. Sepala lanceolata acuminata 20–25 mm longa 4–5 mm lata. Petala rubra anguste lanceolato-elliptica, acuta, 10–16 mm longa, 3–6 mm lata. Filamenta antisepala 14–15 mm longa antipetala 9–11 mm longa, antheris oblongis 3.5–4 mm longis 1.5–2 mm latis. Stylus pilosus, stigmatibus capitatis, 3–4 mm longo, 2.5–3 mm lato apice leviter 4-fisso. Bacca matura non visa.

Scandent shrubs 1.5–3 m high or lianas to 10 m above ground. Young growth finely puberulent-velutinous, branchlets mostly subtriangular in transection. Leaves mostly ternate, occasionally opposite, firmly membranous, narrowly elliptic-ovate, obtuse to rounded or unequal at the base, acute to acuminate at the apex, 5–15 cm long, 1.5–6 cm wide, subglabrous to puberulent above, puberulent below, especially along the veins; secondary veins 9–11 on either side of the midvein; margin subentire to denticulate. Petioles puberulent, 3–20 mm long. Stipules narrowly triangular, ca. 2 mm long, deciduous. Flowers numerous and pendant in terminal racemes; rachis puberulent, 7–16 cm long; bracts 8–50 mm long, 5–25 mm wide, with petioles 1–8 mm long. Pedicels puberulent, 13–50 mm long. Ovary oblong, 7–8 mm long, ca. 2 mm thick. Floral tube subcylindric, 55–76 mm long, bulbous and 3–4 mm wide at the base, then narrowed to 2–3 mm wide above the nectary, slightly widened above until 6–8 mm wide at the rim, puberulent outside, pilose inside. Sepals lanceolate, acuminate, 20–25 mm long, 4–5 mm wide, the tips slightly spreading in bud. Tube and sepals bright red. Petals red, narrowly lance-elliptic, acute, 10–16 mm long, 3–6 mm wide. Nectary unlobed, ca. 2 mm high. Filaments 14–15 mm and 9–11 mm long; anthers oblong, 3.5–4 mm long,

1.5–2 mm wide. Style pilose, stigma 3–4 mm long and 2.5–3 mm wide, 4-parted at the apex. Berry not seen.

Distribution: Known only from the type locality and near vicinity on the eastern slopes of Dept. San Martín, Peru; 2,800–3,600 (Fig. 62).

Specimens examined: PERU, SAN MARTÍN: Valley of Río Apisoncho, 30 km above Jucusbamba, 3,600 m, *Hamilton & Holligan 336* (K, S, UC).

This species belongs to the *Fuchsia simplicicaulis* species group because of its narrowly elliptic-ovate leaves, nearly sessile bracts, and terminally grouped, finely puberulent flowers with petals much shorter than the sepals. It lacks the unusual sessile, concave bracts and involucrate flowers of *F. simplicicaulis* and *F. ceracea*, but it is linked to these species by *F. coriacifolia*, which has an intermediate type of inflorescence, with the older flowers verticillate and the younger flowers alternate.

Hamilton & Holligan 1157 (K), from the type locality, differs from the previously cited specimens of this species in its longer, redder pubescence, shorter petals (6–8 mm long), and much more spreading sepal tips. There are presently too few specimens available to know if this collection falls within the normal variability of *F. sanmartina*.

44. *Fuchsia sessilifolia* Benth., Pl. Hartw. 176. 1845. Hook., Bot. Mag. t. 5907. 1871. Munz, Proc. Calif. Acad. Sci. IV. 25:67, pl. 11, fig. 57. 1943; Opera. Bot., Ser. B, 3:22. 1974. TYPE: Ecuador, Prov. Pichincha, woods of Guayán, W slopes of Volcán Pichincha, 1841–1843, *Theodor Hartweg 985* (K Benth. Herb., holotype; photograph, MO; BM, BREM, CGE, K Hooker Herb., OXF, isotypes).

Erect to scandent shrubs 0.5–3 m tall with few, erect to mostly arcuate branches. Young growth finely puberulent, branchlets subtetragonous, cinereous-puberulent, 2–6 mm thick, wine red; older branches 5–15 mm thick, with exfoliating bark. Leaves verticillate, mostly quaternate, subsessile, membranous to subcoriaceous, narrowly elliptic to elliptic or oblanceolate, rounded to attenuate or narrowly subcordate at the base, acute to acuminate at the apex, 6–20 cm long, 2–6(–8) cm wide, lustrous dark green and subglabrous above, pale green to purplish and pubescent to subglabrous below; secondary veins 18–25 on either side of the midvein, impressed above, the midvein prominent below; margin serrulate and commonly undulate. Petioles 1–5 mm long, dull red. Stipules triangular, thickened at the base, 1–2 mm long, ca. 1 mm wide, mostly deciduous. Flowers numerous in terminal, drooping, verticillately-branched panicles; rachis 5–30 cm long, bracts lanceolate, 10–35 mm long, 4–10 mm wide, often reflexed. Pedicels slender, strigillose, 3–5(–8) mm long. Ovary cylindrical, 5–6 mm long, 1.5–2.5 mm thick, finely strigose. Floral tube narrowly funnelform, 13–18(–20) mm long, 2–3 mm wide at the base, narrowed slightly to 1–2 mm above the nectary, gradually widened above until 4–5 mm wide at the rim, finely strigose outside, pilose inside. Sepals lanceolate, 8–11 mm long, 3–4 mm wide, acute to acuminate, forming a short point 1–2 mm long in bud, spreading at anthesis. Tube pale cream to rose green or light red; sepals light yellow green to light pink. Petals bright scarlet,

contrasting with the lighter sepals and tube, elliptic-oblong, 6–9 mm long, 3–4 mm wide in the middle, acute to rounded at the apex, spreading at anthesis. Nectary unlobed, ca. 1 mm high. Filaments red to greenish red, 5–8 mm and 3.5–5 mm long; anthers oblong, 1.5–2 mm long, ca. 1 mm wide, pale yellow. Style glabrous to loosely pilose; stigma capitate, 4-parted at the apex, 1.5–2 mm long, 1.5–2 mm wide, cream, situated at the level of the anthers or slightly exerted. Berry cylindric-oblong, 15–19 mm long, 8–11 mm thick, green to nitid purple; seeds reddish purple to tan, 1.5–2 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Ecuador and Colombia. In the Cordillera Occidental of the Northern Andes from Pichincha, Ecuador to Chocó and Antioquia, Colombia; in the Cordillera Central from northern Napo to Tolima; and in the Cordillera Oriental from Putumayo to Huila; cloud forest shrubs in thickets, streambanks, and forest openings; 2,300–3,200 m (Fig. 63).

Representative specimens examined: COLOMBIA, ANTIOQUIA: without locality, *Kalbreyer in 1879* (K). CAQUETÁ: Pass between Garzón and Florencia, *Mason 13930* (COL, GH, UC, US). CAUCA: above Carpintería, *Alston 8232* (BM, COL, RSA, S, US); between Guachicono and Río Putis, *Core 936* (MICH, RSA, US); Finca La Cumbre, headwaters of Río Dinde, *Core 1086a* (US); Quebrada de Santo Domingo, headwaters of Río Palo, Cordillera Central, *Cuatrecasas 19297* (A, F, NY, VALLE); Aguabonita, region of Moscopán, east slopes Cordillera Central, *Cuatrecasas 23555* (F, RSA); Vinagrita tibia, Puracé, *Dryander 1633* (US); west slopes of Río Munchique, *García-Barriga et al. 12928* (AAU, COL, US); W of Tambo, Cordillera Occidental, *Haught 5191* (COL, P, RSA, US); Páramo de Las Papas, between El Boquerón and La Hoyola, *Idrobo et al. 3919* (COL, P); Volcán de Sotará, *Lehmann 6220* (K); Canaan, Puracé, *Pennell & Killip 6674* (GH, NY, PH, US); Paletara to Calaguala, *Pennell 7111* (GH, NY, PH, US); San José, San Antonio, *Pennell 7569* (GH, NY, PH, US); above Carpinterías, between Cerros Munchique and Altamira, *Pérez-Arbelaes & Cuatrecasas 6145* (COL, F, US); valle de Quintero, near Pitaió, Río Palo basin, *Pittier 1427* (NY); road from Tambo to 20 de julio, *Plowman & Vaughan 5315* (COL). CHOCÓ: headwaters of Río Carmen, 8 km N of Carmen de Atrato, *Fosberg 21560* (RSA, US); Dauro, *Toro 1168* (NY). HUILA: Km 25 of Pitalito-Mocoa road, *Berry 3592* (COL, MO); between Gabinete and Andalucía, *Cuatrecasas 8586* (COL, F, US); Finca Merenberg, Municipio de La Playa, *Díaz Piedrahita et al. 405* (COL); Lavaderos, ridge between Ríos Naranjo and Granadillo, 15 km S of San Agustín, *Fosberg 20062* (RSA, UC, US); 20 km from Altamira toward Florencia, *Luteyn et al. 4846* (COL, MO); between Garzón and Florencia, *Mason 13921* (UC); E of Neiva, *Rusby & Pennell 687* (NY, US). NARIÑO: above El Encano, Laguna La Cocha, *Balls 7521* (BM, COL, K, NA, UC, US); between Pasto and Río Bobo, *Barclay 4670* (COL, MO); Gruta de la Virgen, road Pasto to Yacuanquer, *Benavides 31* (PSO); Aponte, Río Majinsanoy, *Bristol 1177* (COL, DS); right bank of Río Barrancos, Municipio de La Florida, *Díaz et al. 831* (COL); Encano, N end of Laguna La Cocha, *Fosberg 20431* (RSA, S, US); Laguna La Cocha, Isla La Corota and Sixce-Turibamba, *García-Barriga et al. 13049* (COL, US); woods near Pasto, *Jameson 432* (BM, CGE, G, K, LE, OXF, TCD); road from Cuatro Esquinas to Quitasol, *Mora 293* (COL); road from Balalaika to Yascual, *Mora 396* (COL); near crossroads of El Pedregal-Ipiales road, Guacuán path, *Mora et al. 6056* (PSO). PUTUMAYO: 2 km SW of Sibundoy, *Bristol 328* (COL, DS, GH); Km 79 from Pasto to San Francisco and Mocoa, *Plowman & Davis 4315* (COL); Páramo de San Antonio, road Pasto-Sibundoy, *Schultes & Cabrera 18883* (US); near Sibundoy, *Schultes & Smith 3061* (BH, DS, MO, NY, UC). QUINDÍO: 12 km from Salento towards Cocora, along Río Salento, *Escobar 1014* (MO). TOLIMA: Buenavista, *André 2134* (F, GH, K, NY); Quindío, *Triana s.n.* (G 2 sheets, P); Mt. Quindío before El Gallego, *Triana 6125.6* (BM, COL). VALLE: Barragán, watershed of Río Bugalagrande, La Laguna, *Cuatrecasas 20863* (F, RSA, VALLE); La Palma, right bank Río Pichindé, watershed of Río Cali, *Cuatrecasas 21672* (F, RSA, VALLE); Río Cali, Pichindé, *Duque-Jaramillo 4702* (COL); near Palmira, near Quebrada El Socorro, Cordillera Central, *Maas & Escobar 628* (MO, U). ECUADOR, CARCHI: Km 57 of Tulcán-Maldonado road, *Boeke 828* (MO); 5 km W of El Carmelo, *Berry 3163* (MO, QCA); El Pun (= El Carmelo), *Asplund 16890* (K, NY, S), *Mexia 7579* (POM, RSA, UC, US). IMBABURA: Urcusique, W slopes of Volcán Cotacachi, *Acosta Solis 8225* (F). NAPO: Santa Bárbara de Sucumbios, along Colombia border, *Harling 4130* (NY, S); Río San Pedro below mouth of Río Clavadero, E of Cayambe peak, *Wiggins 10454* (DS). PICHINCHA: Guarumal, Km 38 of road to Saloya, *Acosta Solis 11008* (F); Saloya, W of Quito, *Asplund 7302* (S); Chiriboga, *Asplund 17146*

(NY, S); near Atahualpa, *Asplund* 20314 (NY, S); above Chaupi-Saycha, Pululagua, *Bell* 513 (BM); above San José de Minas, *Benoist* 3963 (F); 41 km W of Cotocollao to Nanegal, *Berry & Escobar* 3182 (MO, QCA); 34 km W of Chillogallo to Chiriboga, *Berry & Escobar* 3242 (MO, QCA); Cornejo Astorga, road Quito-Santo Domingo de los Colorados, *Harling et al.* 9355 (MO, RSA); below Nono, *Haught* 3166 (A, BH, US); above Tandapi, *Holm-Nielsen et al.* 7130 (AAU); Alaspongo, *Holmgren & Heilborn* 697 (S); Mt. Corazón and Lloa, *Sodiño s.n.* (W); San Ignacio, road Aloag-Santo Domingo, *Sparre* 14596 (S); Km 37–50 along Río Saloya, between Volcanes Atasco and Pichincha, *Steyermark* 52513 (NY).

This is an easily recognizable species due to its large, lanceolate, subsessile, and quaternate leaves and the terminal, drooping panicles of short, pale flowers with contrasting dark petals. It is one of the most widespread species in the genus, occurring in Ecuador on both sides of the Andes and in all three cordilleras of the northern Andes. Its distribution pattern indicates a probable origin in the Cordillera Occidental of Ecuador with a subsequent northward extension into the southern parts of the Colombian cordilleras. As a result of this wide distribution, it is sympatric with many taxa of *Fuchsia*, including *F. cuatrecasasii*, *F. corollata*, *F. dependens*, *F. hartwegii*, *F. nigricans*, *F. scabriuscula*, *F. sylvatica*, *F. polyantha*, and *F. verrucosa*. It is only known to hybridize with *F. nigricans* (see discussion under that species).

Fuchsia sessilifolia has flowers similar to *F. nigricans* in the contrasting petal and tube colors, short tubes, and cylindrical ovaries, but it has a much more branched inflorescence. It is very closely allied to *F. polyantha*, which can only be distinguished by its longer, totally red flowers. The two species occur together or in close proximity on the western slopes of the Ecuadorian Andes, and their different floral tube lengths and flower coloration may be related to different pollinators, or to the development of mechanical factors that reduce the chance of interspecific pollination.

45. *Fuchsia polyantha* Killip ex Munz, Proc. Calif. Acad. Sci. IV. 25:48, pl. 7, fig. 37. 1943. Munz, Opera Bot., Ser. B, 3:21. 1974. TYPE: Colombia, Dept. Nariño, between Mayasquer and Tambo, 2,800 m, 2 Aug. 1935, *Ynes Mexia* 7571 (US 1662416, holotype; photographs, NY, POM; F, UC, US, isotypes).

Erect shrubs 1–2 m tall. Young growth minutely puberulent-canescens; branchlets puberulent, terete, purplish. Leaves quaternate, firmly membranous, narrowly elliptic-lanceolate, acute to obtuse at the base, acuminate at the apex, 7–12 cm long, 2.5–4 cm wide, nitid dark green and subglabrous above, light green and sparsely puberulent below, especially along the veins; secondary veins 13–16 on either side of the midvein; margin subentire to serrate. Petioles puberulent, purplish, 3–10 mm long. Stipules dark, thick at the base, triangular, 1.5–2 mm long, ca. 1 mm wide, often connate and recurved when old, persistent. Flowers numerous in terminal, nodding, verticillately branched panicles; rachis 8–15 cm long; bracts narrowly lance-ovate, recurved, 10–30 mm long, 5–10 mm wide. Pedicels puberulent, 5–10 mm long. Ovary fusiform, puberulent, 6–7 mm long, ca. 2 mm thick. Floral tube narrowly funnelform, 34–43 mm long, slightly nodose and 2.5–3.5 mm wide at the base, narrowed to ca. 2 mm above the nectary, then widened above until 5–7 mm wide at the rim, finely puberulent outside, pilose inside in lower ½. Sepals narrowly lanceolate, acuminate, 10–15 mm long, ca. 3 mm wide, with a narrow tip 1.5–2 mm long in bud. Tube and sepals red. Petals

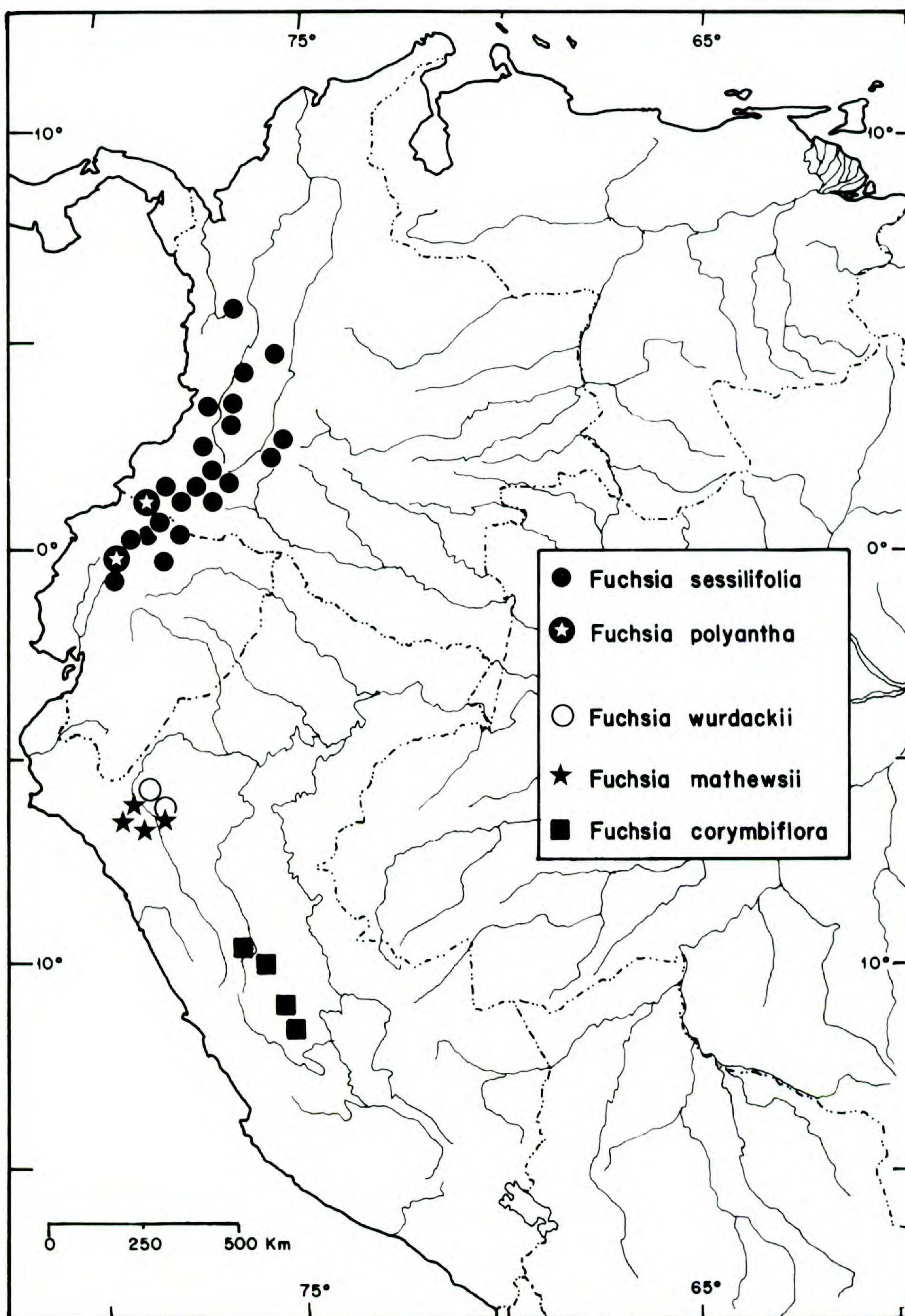


FIGURE 63. Distribution of the *Fuchsia sessilifolia* species group and part of the *F. boliviana* species group.

red, a little darker than the sepals, lanceolate to narrowly elliptic, subacuminate, 8–14 mm long, 2.5–4 mm wide. Nectary unlobed, ca. 1 mm high. Filaments red, 8–11 mm and 6–7 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide. Style red, sparsely pilose in lower $\frac{1}{2}$; stigma capitate, slightly 4-parted at the apex, 2–3 mm long, ca. 2 mm wide, dull white, exserted 3–4 mm beyond the anthers. Mature berries not seen, young ones oblong, 8–10 mm long, 5–7 mm thick. Gametic chromosome number $n = 11$.

Distribution: Western slopes of the Cordillera Occidental from Nariño, Colombia south to Pichincha, Ecuador; rare in cloud forest, 2,200–3,300 m (Fig. 63).

Specimens examined: ECUADOR, CARCHI: 50 km W of Tufiño on road to Maldonado, *Berry 3152* (MO, QCA); 60 km W of Tufiño to Maldonado, *Berry 3154* (MO, QCA); 20 km E of Maldonado on road to Tulcán, *Gentry & Shupp 26321* (MO); between Morán and Olivos, *Mexia 7474* (US). PICHINCHA: Km 32–38 of old road from Quito to Santo Domingo de los Colorados, *Luteyn & Lebrón-Luteyn 5620* (MO, NY).

Except for its longer, entirely red flowers, this species is very similar to the more widespread and apparently sympatric *Fuchsia sessilifolia*. They both have distinctive subsessile, narrow, quaternate leaves with a well branched, terminal, drooping inflorescence. No plants with intermediate flower tube sizes or colors have been seen, and the two species may be reproductively isolated by different pollinators. The floral tubes of *F. sessilifolia* are greenish and less than 20 mm long, while those of *F. polyantha* are red and 34–43 mm long.

- 46. *Fuchsia tineta*** I. M. Johnston, J. Arnold Arbor. 20:242. 1939. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):565. 1941, pro parte. Munz, Proc. Calif. Acad. Sci. IV. 25:43, pl. 6, fig. 32. 1943, pro parte. TYPE: Peru, Dept. Cuzco, Prov. Paucartambo, Río Tambomayo, 1,800–2,000 m, 25 July 1936, *James West 7092* (UC, holotype, not seen; photograph of GH isotype, NY; GH, MO, isotypes).

Erect subshrubs 0.5–1.5 m tall. Young growth whitish pilose, turning tan to reddish-brown with age; older stems 4–10 mm thick, with light brown, striated bark. Leaves opposite or sometimes subopposite near the branch tips, softly membranous, ovate-elliptic to broadly ovate, acute to rounded or unequal at the base, acute to acuminate at the apex, 3–14 cm long, 1.5–9 cm wide, velvety dark green and strigillose above, pale green or commonly purple flushed and strigose below, pubescence denser along the nerves; secondary veins 11–18 on either side of the midvein, sulcate above; margin glandular-denticulate to coarsely dentate. Petioles strigose, 13–50 mm long. Stipules lanceolate, dark, 1–2 mm long, subpersistent. Flowers usually 5–10 and nodding in a generally compact, terminal, corymbose raceme; rachis 1.5–7 cm long. Pedicels slender, strigose, 18–30 mm long, ascending in bud to divergent at anthesis. Ovary cylindric-fusiform, 6–8 mm long, 1–2 mm thick. Floral tube narrowly funnelform, 16–23 mm long, 1.5–2.5 mm wide and slightly bulbous at the base, narrowed to 1–1.5 mm above the nectary, then widened gradually above until 3–5 mm wide at the rim, pilose outside, retrorse villous inside in lower $\frac{1}{2}$. Sepals lanceolate, 7–9 mm long, 3–4 mm wide, acute, spreading at anthesis. Tube and sepals pink to bright red. Petals pink to red, oblong, 6–9 mm long, 3–5 mm wide, obtuse to mucronate at the

TABLE 13. Principal morphological differences between *Fuchsia tincta* and *F. vargasiana*.

	<i>F. tincta</i>	<i>F. vargasiana</i>
Leaves:		
Shape	Broadly elliptic-ovate	Narrowly elliptic-ovate to deltoid
Color	Dark green above, mostly purple flushed below	Medium-dark green above, pale green below
Flowers:		
Tube length	12–23 mm	35–40 mm
Sepal color	Red pink	Dull green
Sepal and petal angle at anthesis	Spreading	Strongly spreading to divergent
Fruits:		
Shape	Ellipsoid to subglobose	Narrowly cylindrical, often curved and with a constricted apex
Length when ripe	13–17 mm	25–32 mm

apex, spreading at anthesis. Nectary unlobed or shallowly 4-lobed, ca. 1.5 mm high. Filaments pink to red, 5–7 mm and 3–4 mm long; anthers oblong, ca. 2 mm long, ca. 1.2 mm wide, white. Style light red, retrorse villous in lower $\frac{2}{3}$; stigma capitate, 1.5–2 mm long, 1.5–2 mm wide, 4-parted at the apex, white to light pink, exserted 2–3 mm beyond the anthers. Berry ellipsoid to subglobose, 13–17 mm long, 8–11 mm thick; seeds 1.4–1.6 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Endemic to Dept. Cuzco, Peru. Locally common in damp, shady thickets along streams and roadsides, on the eastern slopes of the Andes in the Pillahuata area, between Paucartambo and Pilcopata; also known from Prov. Convención farther north; 1,800–2,400(–2,800) m (Fig. 62).

Specimens examined: PERU, CUZCO: Km 131–137 of Cuzco-Pilcopata road, near Buenos Aires, *Berry et al.* 2597 (MO, USM), 3004 (MO, USM), 3006 (MO, USM); Pillahuata, Cerro de Cusilluyoc, *Pennell* 13956 (F, GH, PH, S, US); above Pintobamba, Prov. Convención, *Vargas* 3551a (BH, CUZ); Pillahuata, *Vargas* 5128 (BH, CUZ, MO); Ticancha, Huaisanpilla, *Vargas* 9922 (CUZ, MO); Pillahuata, Yanamayo, *Vargas* 16695 (CUZ, RSA), 16703 (CUZ, RSA), *Woytkowski* 2 (MO, USM); between Puente Mercurio and Buenos Aires, *Vargas* 23138 (MO); Suecia, *Woytkowski* 144 (USM).

This species is closely allied to *Fuchsia vargasiana* and *F. furfuracea*, which share the compact, terminal racemes, dense pubescence, and similar ovate, long-petiolate leaves. *Fuchsia tincta* has shorter flowers than these two species, though, and usually has deep dark green leaves with a purple flush below.

It is remarkable that *F. tincta* and *F. vargasiana* are so similar morphologically, yet they are sympatric and occupy the same restricted range. Both are diploid and grow together in the same thickets at ca. 2,100 m (Km 136–137) along the Paucartambo-Pilcopata road, flowering simultaneously. Despite this, no apparent hybrids or morphological intermediates were found either in the field or

TABLE 14. Comparison of the principal morphological differences between *Fuchsia tincta*, *F. sanctae-rosae*, and a presumed hybrid.

	<i>F. tincta</i>	Hybrid (Pennell 13956, NY)	<i>F. sanctae-rosae</i>
Leaves:			
number/node	2	2–3	3–4
Max. blade size (L × W)	14 × 9 cm	15 × 6 cm	14 × 4 cm
Pubescence, lower surface	Strigose on entire surface	Strigose mostly along veins	Glabrous except hairs on midvein
Flowers:			
Position	Racemose	Axillary	Axillary
Tube pubescence outside	Pilose	Strigose-pilose	Glabrous
Pubescence on young growth	Whitish pilose	Canescent	Subglabrous

in herbarium specimens. An enumeration of the main differences between *F. tincta* and *F. vargasiana* is presented in Table 13.

Fuchsia tincta is also sympatric with *F. sanctae-rosae*. Pennell 13956 (NY), from Pillahuata, is apparently a hybrid between these two species. Diagnostic characters of the putative hybrid and the parental species are given in Table 14. A pollen stainability of 9.2% (500 grains examined) for this collection further supports the hypothesis that it is of hybrid origin.

47. *Fuchsia furfuracea* I. M. Johnston, Contr. Gray Herb. 75:39. 1925. Munz, Proc. Calif. Acad. Sci. IV. 25:46, pl. 6, fig. 34. 1943. TYPE: Bolivia, Dept. La Paz, Yungas, 1890, Miguel Bang 674 (BH, holotype; photographs, POM, UC; F, K, MO, NY, PH, US, isotypes).

Erect to scandent shrubs 0.5–2.5 m tall. Young growth densely hispidulous to tomentose with suberect, whitish hairs often becoming tan or ferrugineous with age or drying; branchlets subterete, 2–4 mm thick, green or reddish; older branches 5–10 mm thick, loosely hirtellous, with smooth, purple tan bark. Leaves opposite or rarely ternate, membranous, elliptic-ovate, rounded to acute at the base, acuminate and often curved at the apex, 6–15(–17) cm long, 3–6(–7) cm wide, matte dark green and hispidulous-strigose above, slightly paler to flushed purple and hispidulous below, especially along the nerves; secondary veins 9–14 on either side of the midvein, subelevated below; margin serrulate to denticulate. Petioles pubescent, 2–5(–7) cm long. Stipules lance-linear, acuminate, dark, 2–3 mm long, 0.2–0.4 mm wide. Flowers few and pendant in short, corymbiform, terminal racemes; rachis 1.5–5 cm long with bracts 10–25 mm long. Pedicels slender, pubescent, 15–40 mm long, lengthening considerably from bud to fruit. Ovary ellipsoid-oblong, 5–8 mm long, 2–3 mm wide, densely pubescent. Floral tube narrowly funnelform, (22–)25–48 mm long, 2–3 mm wide and slightly nodose at the base, constricted to 1.5–2 mm wide above the nectary, gradually widened above until 6–9 mm wide at the rim, hispidulous outside, villous inside for most its length. Sepals lanceolate, 10–18 mm long, 3–5 mm wide, mostly long acuminate with free tips in bud for 1–3 mm, spreading at anthesis. Tube dull pink to lavender

TABLE 15. Comparison of morphological characters in *Fuchsia furfuracea*, *F. sanctae-rosae*, and presumed hybrids.

	<i>F. furfuracea</i> (6744, BM, F) ¹	Hybrids (6653, BM, F) and (6693, BM) ¹	Hybrids (6719, BM, F) ¹	<i>F. sanctae-rosae</i> (6653, NY) and (6693, F, NY) ¹
Stem pubescence	Densely pilose, reddish hairs	Loose villous	Loose villous	Glabrous
Leaf shape	Broadly ovate	Lance-elliptic	Narrowly elliptic	Narrowly elliptic
Leaf pubescence	Strigillose on both sides	Densely villous on veins below	Villous on both sides	Glabrous except hairs on mid- vein below
Leaf margin	Serrulate	Lightly serrulate	Serrulate	Entire
Number of secondary veins	11–18	10–16	11–12	5–10
Inflorescence type	Tight terminal ra- ceme 1–4 cm long	Subracemose, 6– 12 cm long	Subracemose, 8– 16 cm long	Axillary along uppermost 25 cm of branches

¹ All numbers refer to W. Brooke collections from Incachaca, Dept. Cochabamba, Bolivia, collected in Aug. 1950.

or orange red; sepals light red but becoming pale white toward the tips. Petals bright pink red to dark red, elliptic-ovate, mostly about ½ as long as the sepals, 6–10 mm long, 3–5 mm wide, acute at the apex, suberect at anthesis. Nectary unlobed or shallowly 4-lobed, ca. 1.5 mm high. Filaments lavender, 7–8 mm and 4–5 mm long; anthers oblong, 2–3 mm long, 1–1.5 mm wide. Style villous from the base to near the rim of the tube; stigma capitate, 4-cleft at the apex, 2–3 mm long, 2–3 mm wide, white. Berry ovoid-ellipsoid, becoming subglobose when fully ripe, 12–16 mm long, 6–12 mm thick, pubescent; seeds ca. 1.5 mm long, ca. 1 mm wide.

Distribution: Bolivia. Rare shrubs growing mostly in dripping wet sites such as cliff overhangs and along rivulets in cloud forest of Depts. La Paz and Cochabamba; 2,800–3,050 m (Fig. 62).

Specimens examined: BOLIVIA, COCHABAMBA: Incachaca, *Brooke 6744* (BM, F). LA PAZ: San Felipe, Sur Yungas, *Asplund 1743* (UPS); near Chuspipata, Km 65 of La Paz-Beni RR, *Barker 220* (US); valley of Zongo, Prov. Murillo, *Beck 2173* (MO); 9 km from Unduavi on road to Coroico, *Berry 2577* (MO); Unduavi, *Cárdenas 3617* (RSA); Carretera Fundamental 3, 27 km SW of Yolosa junction, *Davidson 4937* (MO); Unduavi, *Rusby 2511* (NY); 20 km SW of Yolosa junction toward Unduavi, *Solomon 4860* (MO), *4865* (MO); Yungas valley, *Tutin 1391* (BM); 19 km from Unduavi to Coroico, *Vargas 22057* (CUZ); Prov. of Yungas, *Weddell 2291* (P); valleys between Tipuani and Apolobamba, Prov. Larecaja and Caupolicán, *Weddell 4601* (P). WITHOUT LOCALITY: *Bridges 283* (LE), in 1846 (BM, CGE, K); *Cuming 229* (W), *s.n.* (W).

The few-flowered, compact, terminal inflorescences and mostly opposite, pubescent, long petiolate, ovate leaves closely ally this species to *Fuchsia tincta* and *F. vargasiana*, both of which are endemic to southern Peru. The flowers of *F. furfuracea* are larger than those of *F. tincta*, and the fruits are shorter than those of *F. vargasiana*. *Fuchsia furfuracea* is further characterized by its elongate stipules, mostly ferrugineous hairs on older growth, and pale sepals usually about twice as long as the petals.

All three species in the *F. tincta* species group have a very restricted range.

TABLE 16. Pollen stainability of *Fuchsia furfuracea*, *F. sanctae-rosae*, and suspected hybrids.¹

Taxon	Stainability ²
<i>Fuchsia furfuracea</i> (Brooke 6744, BM, F)	88.4%
Hybrid (Brooke 6693, BM)	0%
Hybrid (Brooke 6719, BM)	20%
Hybrid (Brooke 6653, F)	8.6%
<i>Fuchsia sanctae-rosae</i> (Brooke 6653, NY)	83.8%

¹ All specimens collected in Aug. 1950, around Incachaca, Dept. Cochabamba, Bolivia.² 500 grains counted for each collection.

Fuchsia furfuracea is known from a few localities in the “yungas,” or moist, cool valleys of the northeastern slopes of the Bolivian Andes, and it is furthermore restricted to very moist habitats such as streamsides or near waterfalls.

Weddell 4061 (P), from Prov. Larecaja near the Peruvian border, has floral tubes just 22 mm long and is distinguishable from *F. tinctoria* only by its slightly longer, browner pubescence and proportionately shorter petals. There are no other collections from the Peru-Bolivia border area, however, to indicate if more intergradation between these two species occurs there.

In Dept. La Paz, *Fuchsia furfuracea* is found close to, but at higher elevations than *F. boliviana* and *F. sanctae-rosae*; it occurs at lower elevations than *F. denticulata*. In Dept. Cochabamba, a series of probable hybrids with *F. sanctae-rosae* were collected by Winifred Brooke in 1950 around Incachaca. Intermediate morphological traits of the putative hybrids are compared to those of the presumed parents in Table 15, and Table 16 shows the strongly reduced pollen stainability of the same intermediates. I returned to Incachaca in July 1979 and found plants of *F. sanctae-rosae* abundant in weedy thickets, but no trace of *F. furfuracea*. The valley at Incachaca is now mostly cleared or covered by secondary vegetation, and *F. furfuracea* is confined to more heavily forested areas.

- 48. *Fuchsia vargasiana*** Munz ex Vargas, Diez Años Servic. Bot. Univ. Cuzco, 50, fig. 16. 1946. TYPE: Peru, Dept. Cuzco, Prov. Paucartambo, between Yanamayo and Tambomayo, 2,000 m, 25 July 1936, César Vargas C. 73 (BH, holotype; CUZ, F, MO, POM, isotypes). On the type sheet, Vargas indicated that the same plant was collected by James West, under a separate number, *West 7110* at GH and UC.

Fuchsia tinctoria sensu J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):564. 1941, pro parte, sensu Munz, Proc. Calif. Acad. Sci. IV. 25:43. 1943, pro parte.

Erect shrubs 1–2 m tall. Young growth finely soft pilose with white to rusty hairs; older branches 4–10 mm thick, dull tan-brown. Leaves opposite, membranous, narrowly ovate-elliptic to narrowly subdeltoid, rounded to obtuse or unequal at the base, acuminate at the apex, 6–23 cm long, 2.5–9 cm wide, subnitid dark green and sparsely strigose to subglabrous above, pale green below and finely pilose mostly along the veins; secondary veins 12–18 on either side of the midvein; margin glandular-serrulate or denticulate. Petioles pubescent, 12–60 mm long. Stipules lanceolate, dark, 1–2 mm long, ca. 0.4 mm wide, deciduous. Flow-

ers usually 3–10 in terminal, corymbose racemes; rachis 2–8 cm long, at times with reduced leaves subtending the flowers. Pedicels ascending when young to divergent-drooping at anthesis, 10–35 mm long. Ovary narrowly cylindrical, puberulent, 10–11 mm long and ca. 2 mm thick. Floral tube narrowly funnelform, 35–40 mm long, 2–3.5 mm wide and slightly nodose at the base, narrowed to 1.5–2.5 mm above the nectary, then gradually widened above until 4–8 mm wide at the rim, pilulose outside, villous inside in lower $\frac{2}{3}$. Sepals lanceolate, acuminate, 11–16 mm long, 4–5 mm wide, with a short tip 1–2 mm long in bud, strongly spreading to divergent at anthesis. Tube red, sepals green except for the reddish base. Petals red, oblong to broadly elliptic, 10–12 mm long, 5–8 mm wide, rounded and usually with a short point at the apex, strongly spreading at anthesis. Nectary unlobed, ca. 2 mm high. Filaments red, 6–10 mm and 4–8 mm long; anthers oblong, 2–3 mm long, 1–1.5 mm wide, white. Style red pink, villous from the base to near the rim of the tube; stigma capitate, ca. 2 mm long and wide, 4-parted at the apex, white to dull pink. Berry narrowly cylindrical-fusiform, often curved and usually constricted at the apex, 25–32 mm long, ca. 8 mm thick; seeds 1.3–1.6 mm long, 0.9–1.1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Endemic to Dept. Cuzco, Peru. Locally frequent in moist shady thickets along the Río Tambomayo, Pillahuata area of Prov. Paucartambo; 1,700–2,300 m (Fig. 62).

Specimens examined: PERU, UZCO: Km 132–140 of Cuzco-Pilcopata road, below Buenos Aires, *Berry et al.* 3000 (MO, USM), 3003 (MO), 3005 (MO, USM); between Yanamayo and Santa Isabel, valley of Río Cosñipata, *Scolnik* 851 (RSA); Tambomayo, *Vargas* 22986 (MO); Pillahuata, *Vargas* 22985 (MO); Suecia, *Woytkowski* 128 (USM).

This species is closely related to the sympatric *Fuchsia tinctoria* and to the Bolivian *F. furfuracea*. It has distinctive long, fusiform, curved fruits and narrower leaves than either of the above species, and its sepals are green-tipped. Its sympatric occurrence and apparent lack of intermediates with *F. tinctoria* are discussed under that species, and a comparison of their distinguishing characters is presented in Table 13.

The label of *Vargas* 4524 (BH) records the collection locality as “Dept. Cuzco, Prov. Convención, 3,600 m,” but this is probably in error, since it is very unlikely that this species would occur at so high an elevation. *Fuchsia vargasiana* is sympatric with *F. sanctae-rosae*, *F. tinctoria*, and populations of *Fuchsia* related to *F. denticulata* (Fig. 11).

49. *Fuchsia boliviana* Carrière, Rev. Hort. 48:150, pl. 1876. Hemsl., Garden 11:70, pl. 1877. Johnst., Contr. Gray Herb. 75:37. 1925. Fawc. & Rendle, Fl. Jamaica 5:413, fig. 149. 1926. Travis, Fuchsia Annual 1975:55, photo. 1975. non Britton, 1890. *Fuchsia boliviana* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25:53, pl. 8, fig. 42. 1943. Based on *F. boliviana* Carr. TYPE: Plate in Révue Horticole 48:150. 1876, drawn from plants cultivated in France in 1876 from seeds collected in the mountains of Bolivia at “6000 m” (a probable error for 6,000 ft.) in 1873 by Benedict Roezl. Figs. 34, 43, and 64 (lectotype, here designated).

Fuchsia corymbiflora auct., non Ruiz & Pavón, 1802. Lindl., Bot. Reg. 26: pl. 70. 1840. Harrison,

Florist. Cab. & Florist's Mag. 9: *t. 1*. 1841. Paxt., Paxton's Mag. Bot. 8:7, *pl.* 1841. Hook., Bot. Mag. 69: *pl.* 4000. 1843; Gard. Chron. 1845:192, *fig.* 1845, Sweet, Ornam. Fl. Gard. 1: *t.* 29. 1854. Regel, Gartenfl. 28:241, *fig.* 1879. Sieb. & Voss. in Vilm., Bulmengart. ed. 3, 1:333, *fig.* 1896. Watson, Garden 55:74, *fig.* 1899. Hegi, Ill. Fl. Mittel-Eur. 5(2):801, *fig.* 2189, *a-d.* 1925. Bonstedt in Pareys Blumengart. 2:79, *photo.* 1932. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):551. 1941, *pro parte.*

Fuchsia corymbiflora alba Harrison, Florist. Cab. Florist's Mag. 17:97, *fig.* May, 1849. Paxt., Paxton's Mag. Bot. 16:219. 1849. van Houtte, Fl. Serres Jard. Eur. 6:29, *fig.* 1850. Essig, Nat. Hort. Mag. 13:6, *photo.* 1934. LECTOTYPE: the figure in Harrison, Florist. Cab. Florist's Mag. 17:97. 1849, illustrated from plants grown by John Salter in 1849 in London, England from plants obtained from "Continental Europe."

Fuchsia boliviana var. *luxurians* I. M. Johnston, Contr. Gray Herb. 75:37. 1925. Munz, Proc. Calif. Acad. Sci. IV. 25:54. 1943. TYPE: Venezuela, Edo. Aragua, Colonia Tovar and vicinity, 1,700–2,300 m, 19 Feb. 1921, *Henry Pittier* 9252 (GH, holotype; photograph, UC; NY, US, VEN, isotypes).

Fuchsia cuspidata Fawcett & Rendle, Journ. Bot. 114:105. 1926. TYPE: Jamaica, Blue Mountains, near Woodcutter's Gap, ca. 1,200 m, 10 Aug. 1895, *William Harris* 5825 (BM, holotype).

Fuchsia boliviana forma *puberulenta* Munz, Proc. Calif. Acad. Sci. IV. 25:54. 1943. TYPE: Bolivia, Dept. La Paz, Prov. Nor Yungas, 1,800 m, Dec. 1917, *Otto Buchtein* 732 (F 588700, holotype; photographs, POM, UC; F, G, GH, MO, NY, US, Z, isotypes).

Erect bushy shrubs or small trees 2–4.5(–6) m tall with arching-pendulous branches. Young growth usually densely canescent with fine, erect, gray-white hairs; terminal shoots 2–4 mm thick, terete to angled; older stems woody, usually hollow, 1–6 cm thick, with tan brown, splitting bark. Leaves opposite, ternate, or sometimes alternate near the uppermost branching nodes, softly membranous, narrowly to broadly elliptic or ovate, acute to rounded at the base, acute to acuminate at the apex, 5–20(–23) cm long, 3–12(–15) cm wide, medium to dark matte green and pubescent to subglabrous above, pale green and ashy puberulent to densely canescent below, especially along the nerves; secondary veins (12–)15–25 on either side of the midvein, $\pm$ impressed above, prominent and often reddish below; margin glandular-denticulate. Petioles pubescent, 2–5(–7) cm long. Stipules dark, narrowly lanceolate, 0.5–1.5 mm long, ca. 0.3 mm wide, deciduous. Flowers numerous in terminal, drooping racemes or few-branched panicles, the flowers congested near the tips; rachis 5–30 cm long in flower, 15–40(–60) cm long in fruit; bracts lanceolate, reflexed, 5–25 mm long, 2–8 mm wide. Pedicels slender, pendant, pubescent, 5–12(–16) mm long. Ovary cylindrical, 7–11 mm long, 2–3 mm thick, strigose to puberulent. Floral tube narrowly funnelform (25–)30–60(–70) mm long, 1.5–3 mm wide and slightly bulbous at the base, gradually widened above until 4–7(10) mm wide at the rim, pubescent outside, pilose inside for entire length. Sepals lanceolate, acuminate, 10–20 mm long, 4–5 mm wide, tips apiculate in bud, initially spreading at anthesis, but soon becoming totally reflexed. Tube and sepals pale pink to bright scarlet, rarely pale white. Petals scarlet, acute at the apex, $\pm$ crisate with 2–3 longitudinal ridges, oblong to elliptic, 8–16(–20) mm long, 3–7(–9) mm wide, upper $\frac{1}{2}$ recurved at anthesis, drying and dehiscing before the tube does. Nectary 4-lobed, green, 2–3 mm high. Filaments red, 8–15 mm and 5–10 mm long; anthers oblong, 2–3.5 mm long, 1–1.5 mm wide, white. Style slender, pilose from the base to the rim of the tube; stigma capitate or clavate, subtetragonous, shallowly 4-lobed at the apex, 2.5–3 mm long, 3–5 mm wide, cream, situated at the level of the antesealous anthers or barely exerted beyond them. Berry cylindrical, 10–26 mm long, 8–14 mm thick, dark purple, strigose, comestible; seeds tan, 1.3–2 mm long, 0.5–1 mm wide. Gametic chromosome number $n = 11$.

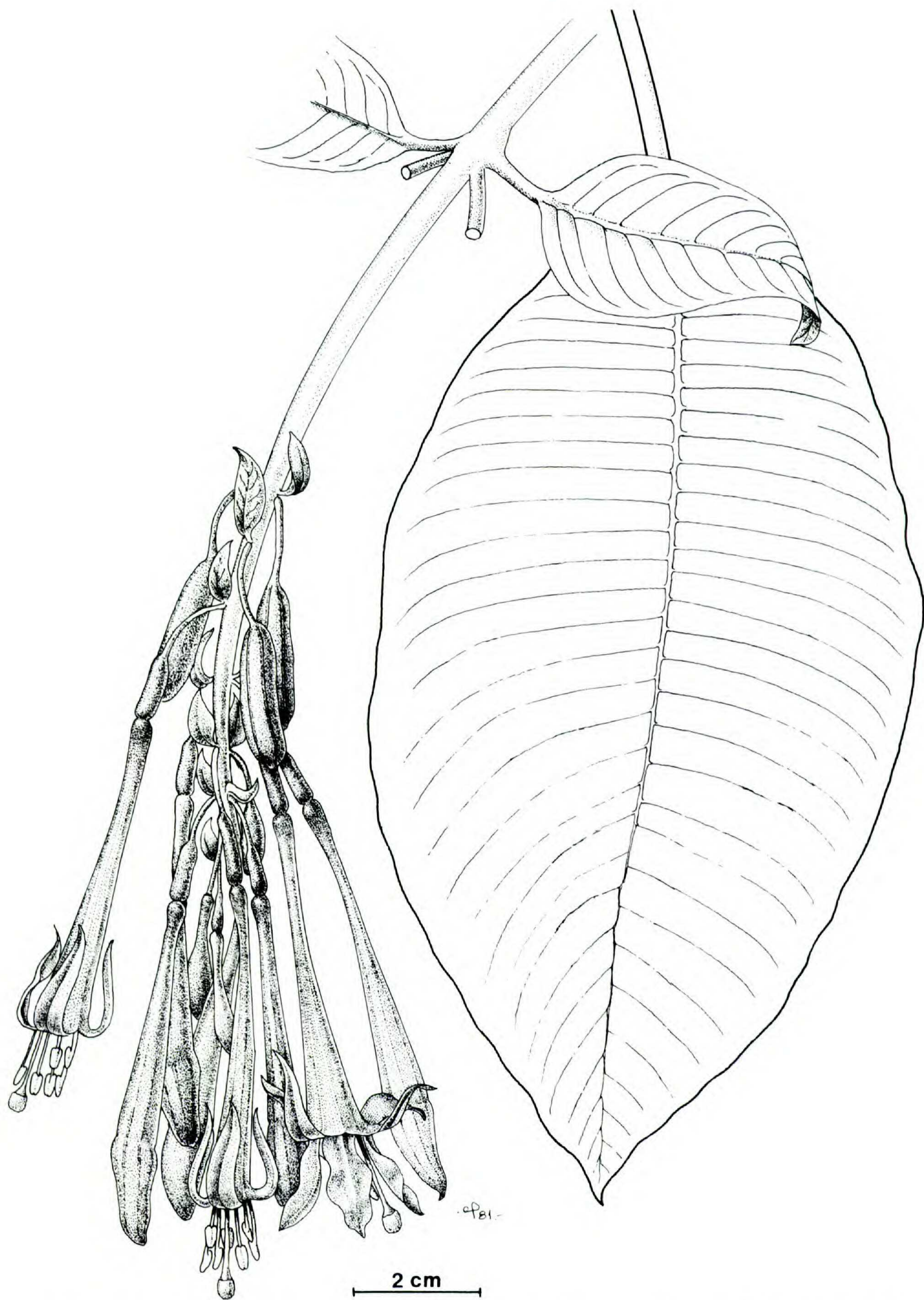


FIGURE 64. *Fuchsia boliviana* Carrière. Drawn from living material from El Portachuelo, D.F., Venezuela.

Distribution: The probable native range extends from northern Argentina to southern Peru, undoubtedly naturalized elsewhere outside South America and in Colombia and Venezuela; cloud forest shrubs in moist thickets; (600–)1,000–3,000 m (Fig. 65).

Representative specimens examined (South America): VENEZUELA, ARAGUA: Colonia Tovar, *Agostini* 65 (VEN), *Allart* 354 (MY, NY, US, VEN), *Berry* 2592 (MO, VEN), *Fendler in 1854–55* (K), *Jahn* 439 (US), *Woronow* 7048 (LE); between El Lagunazo and Colonia Tovar, *Aristeguieta* 781 (VEN), *Trujillo & Fernández* 852 (MY); La Victoria to Colonia Tovar, between Las Moras and Lagunita, *Benítez de Rojas* 566 (MY); Hacienda El Limón, Las Aguaitas, *Delascio* 2057 (VEN); between Colonia Tovar and Pico Codazzi, *Ruiz-Terán & López-Palacios* 10118 (MERF, MO); La Lagunita, near Colonia Tovar, *Schnee* 1309 (MY), ca. 5 km from Colonia Tovar towards El Limón, *Solymosy* S10197150 (VEN). DISTRITO FEDERAL: between El Junquito and Colonia Tovar, *Berry* 2591 (MO, VEN), *Wessels-Boer et al.* 2445 (MO, U); 1–2 km below junction of El Junquito-Colonia Tovar road towards Carayaca, *Cárdenas de Guevara* 433 (MY), *Davidse & Morillo* 3985 (MO), *Luteyn et al.* 5162 (MO, NY); 4 km ENE of Colonia Tovar, *Steyermark* 86212 (MY, NY, VEN). COLOMBIA, ANTIOQUIA: Las Minas, *Barkley* 17C250 (GH); near Boquerón del Toyo, *Barkley & Neira* 17C235 (CAS, COL, GH); canyon 20 km E of Sonsón, road to El Dorado, *Barkley* 38C568 (COL, GH); Alto de Minas, Medellín to La Pintada, *Escobar* 1000 (MO); near San José de San Andrés, *Correa & Velásquez* 68 (COL, RSA, US); between Alto San Miguel and Alto Alegrías, 15 km SSE of Caldas, *Fosberg* 21163 (NY, RSA, US); Alto de Minas, between Caldas and Santa Bárbara, *Garganta* 2003 (US); El Poblado, near Medellín, *Hatheway in 1955* (B); Las Minitas, S of Caldas, *Pennell* 10970 (GH, NY); Cerro del Pedre Amaya, Boquerón, Km 22 of Medellín-Santa Fé de Antioquia road, *Rivera* 808 (PSO). CALDAS: Termales, *Dryander* 2756 (BH, F, VALLE); Manizales, *Sandeman* 5655 (COL, K). CHOCÓ: N of Albán, near Dept. Valle border, *Dugand & Jaramillo* 3046 (US); 2–3 km N of Carmen de Atrato, *Fosberg & Core* 21553 (RSA, US). CUNDINAMARCA: 2.5 km W of Salto de Tequendama, *Barclay et al.* 3303 (COL, NA, US), *Luteyn & Lebrón-Luteyn* 7711 (COL, MO, NY); Bogotá, *Duque-Jaramillo* 3049 (COL, NY), *Pérez-Arbelaes* 4802 (NY, U, US); 17 km W of Mosquera towards La Mesa, *Gentry* 15139 (COL, MO); Km 26–28 SW of La Mosquera towards La Mesa, *Luteyn et al.* 4690 (COL, MO); Zipaquirá, *Pring* 168 (MO); Bogotá, Chapinero, *Schneider* 353-A (COL); 2 km from Zipaquirá on road to Pacho, *Schultes et al.* 3 (GH, K, S, US). SANTANDER: 24 km W of Jordán on Cimitarra-Velez road, *Gentry & Forero* 15466 (COL, MO); 29 km W of Fresno towards Manizales, *Berry* 3552 (COL, MO); above Cajamarca, Giradot-Armenia road, *Berry* 3143 (MO); La Palmilla, Quindío, *Triana* 3812 (G, P); Herveo, *Uribe-Uribe* 756 (COL). VALLE: N of Las Brisas, Carrizales, *Cuatrecasas* 22552 (F, RSA, VALLE). PERU, APURIMAC: Abancay, *Blood & Tremelling* 206 (NA); Chincheros, *Ferreya* 2810 (USM), *Soukup* 6248 (RSA); 8 km E of Abancay, road to Cuzco, *Gentry et al.* 23368 (MO); Ampuy, *Stork et al.* 10595 (A, G, MO, NA, UC); Chirhuay-Matará, *Vargas* 1971 (BH, CUZ, MO); Nacchero, *Vargas* 8962 (CUZ); Huancarema, *West* 3783 (MO, UC). AYACUCHO: 11 km below Jano, road Tambo-Ayna, *Berry* 3057 (MO, USM); Ccarrapa, between Huanta and Río Apurimac, *Killip & Smith* 22280 (NY, RSA, US); above Jano, *Plowman & Davis* 4673 (GH, K); Curahuasi, *Sandeman* 3552 (K, OXF); Ocros, *Vargas* 15912 (CUZ); Prov. La Mar, *Weberbauer* 5555 (F, GH, US). CUZCO: Paucartambo, *Balls* B6715 (BM, K, NA, UC, US), *Plowman & Davis* 4910 (GH); Urubamba, *Berry* 2561 (CUZ, MO), *Herrera* 1058 (GH, US), *Soukup* 28 (F), Km 169 of Cuzco-Quillabamba road, *Berry & Aronson* 3044 (MO, USM); San Miguel, *Chávez* 3108 (MO), *Cook & Gilbert* 915 (US); Hacienda Santa Rita, Urubamba valley, *Dreyfus in 1941* (USM); Machupichu, *Ferreya* 2728 (USM), *Rauh* 773 (RSA), *Vargas* 990 (BH, CAS, CUZ, MO); Lucay, Urubamba valley, *Herrera* 1123 (F, US); Hacienda Churu, Prov. Paucartambo, *Herrera in 1926* (US); Km 105 along RR in Urubamba valley between Ollantaytambo and Machupichu, *Iltis & Ugent* 1132 (DS, GH, K, UC, USM); Punto Real, Urubamba valley, *Tutin* 1308 (BM); Ollantaytambo, *Tutin* 1340 (BM); 5 km NE of Paucartambo on road to Pillahuata, *Ugent & Vargas* 4410 (DS); Huaisanpilla, *Vargas* 9945 (CUZ); Mantla, Km 84, Prov. Calca, *Vargas* 15630 (CUZ); Urubamba valley, between La Máquina and Cedrobamba, *West* 3783 (GH, MICH, MO, NA, RSA, UC, US, USM); Pilco, valley of Río Paucartambo, *Woytkowski* 320 (MO, UC); near Chacra, Prov. Paucartambo, *Woytkowski* 236 (USM). HUÁNUCO: 5 km SE of Carpish, *Stork & Horton* 9921 (F, MICH, MO, RSA, UC, US). PUNO: near Sandia, *Ferreya* 16652 (MO); Oconeque, E of Limbani, *Hodge* 6166 (US); Asalaya, *Vargas* 11812 (CUZ); near Sandia, *Vargas* 14808 (CUZ), 16414 (CUZ), 21246 (CUZ), *Weberbauer* 537 (G), 557 (G). BOLIVIA, COCHABAMBA: Km 205 Cochabamba-Santa Cruz, *Badcock* 382 (K); ca. 60 km from Cochabamba to Villa Tunari, *Berry* 2588-B (MO); Quime, ca. 160 km from Oruro via Eucalyptus, Quimicruz mts., *Brooke* 5385 (BM, F), 5418 (BM); Rosal, near Río Limón, *Brooke* 5706 (BM, F, G, NY, U), 5719 (BM, F); Choro, above Río Cocapata, ca. 160 km NW of Cochabamba, *Brooke* 6076 (BM, F, G, NY, S, U); Incachaca,

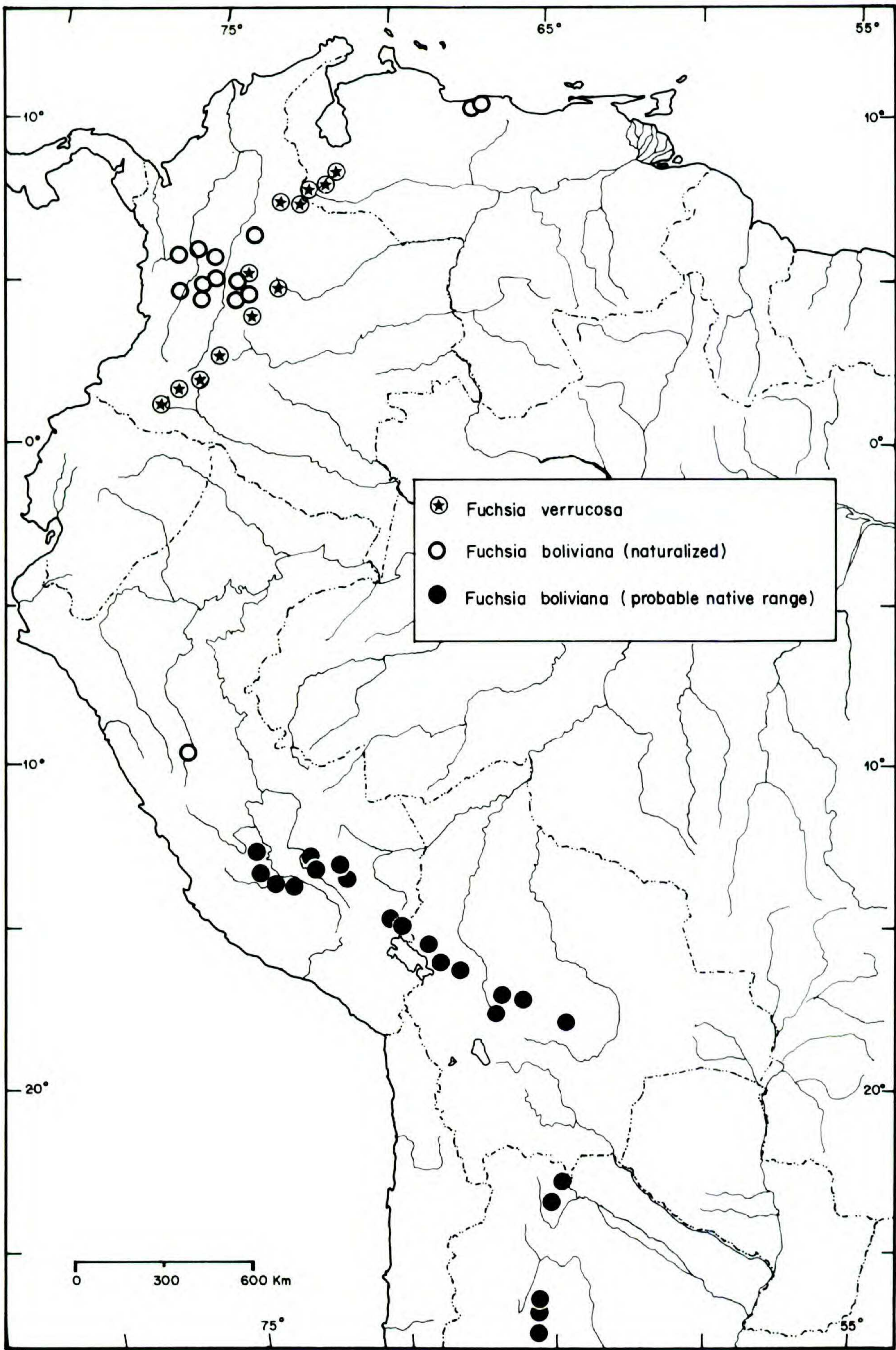


FIGURE 65. Distribution of *Fuchsia boliviana* and *F. verrucosa*.

Brooke 6653 (BM), 6670 (BM, F, NY), 6680 (BM, F), 6719 (BM), *Steinbach* 4306 (K), 5024 (A, G), 5763 (A, F, G, GH, K, MO, PH, US); Parangani, Ayopaya, *Cárdenas* 4086 (GH, RSA); 110 km NE of Cochabamba, near Chimore, S side Río Mateo, *Eyerdam* 24740 (F, UC); Pocona-Tal, *Steinbach* 8781 (BM, GH, K, MO, NY, S); El Limbo, *Steinbach* 537 (G, GH, MO, NY, U, US). LA PAZ: Chungamayo, La Sirena, *Asplund* 317 (UPS); El Chaco, Sur Yungas, *Asplund* 1131 (UPS); Yungas, *Bang* 327 (BM, F, GH, K, LE, MICH, MO, NY, PH, US, W); Zongo Valley, Prov. Murillo, *Beck* 2172 (MO), 2739 (MO); Huancané, Sud Yungas, *Beck* 3066 (MO); 13 km from Unduavi to Coroico, *Berry* 2579 (MO); Chulumani, *Brooke* 6560 (BM); Sirupaya, near Yanacachi, Sur Yungas, *Buchtein* 102 (NY), 218 (NY, US); Sorata, *Cárdenas* 1156 (NY); 15 km SW of Yolosa junction, *Davidson* 4913 (MO); Caranavi, *Ellenberg* 6217 (GOET); near Unduavi, *Eyerdam* 25395 (F, UC); El Chaco, Sur Yungas, *Holway & Holway* 643 (US); between Puente Villa and Chulumani, *Kelley* 1013 (CM, UC); Sacramento, Unduavi to Coroico, *Kelley* 1075 (CM, F, UC); near Sorotá, *Mandon* 622 (BM, F, G, GH, K, LE, NY, P, S, T, US, W); Nor Yungas, *Mexia* 04286 (GH, MO, UC); Colaya, Sur Yungas, *Mexia* 04292 (G, GH, MO, UC), 7809 (F, G, K, MO, S, U, UC, US); near Yungas, *Rusby* 1071 (BM, F, GH, K, LE, MICH, NY, P, PH, US); Okara, *Tate* 908 (NY); Prov. Apopaya, *Weddell* 4179 (P). SANTA CRUZ: Samaipata, *Steinbach* 3755 (GH, POM); Yungas de San Mateo, *Steinbach* 8392 (BM, GH, K, NY, S); Comarapa, *Steinbach* 8459 (BM, GH, K, MO, NY, S). WITHOUT LOCALITY: *Bang* 1806 (BM, F, G, GH, K, LE, MICH, MO, NY, PH, US, W, Z); *Bang* 2005 (BM, F, GH, K, MO, NY, US, W); *Bang* 2833 (F, GH, K, LE, MICH, MO, NY, PH, US). ARGENTINA, JUJUY: road to Valle Grande, Dep. Ledesma, *Cabrera et al.* 22390 (K); San Lorenzo, *Jørgensen in 1911* (POM); 10–20 km from Libertador Gral. San Martín, road to Valle Grande, *Krapovickas et al.* 26668 (MO); Valle Grande, ca. 2 km past Abra de Cañas, *Legname & Cuezco* 8601 (GH); Abra de Cañas, road to Valle Grande, *Vervoorst & Cuezco* 7851 (W). SALTA: San Andrés, *Lorentz & Hieronymus* 265 (G, S), *Pierotti* 312 (A, NY, UC). TUCUMÁN: Quebrada de Las Sosas, *Bocher et al.* 2419 (MO, S), *Killip* 39530 (RSA, US), *Walter & Walter* 621 (B), 653 (B); Casa de Piedras, ca 25 km SSW of Tucumán, *Colaris* 1181 (U); along Río Las Sosas, ca. 60 km SW of Tucumán, *Haas* 893 (U); Sierra de Aconquija, *Humbert* 20929 (P, US); Río Cicerone, *Jørgensen* 21 (GH, MO); Km 20 road to Tafi del Valle, *Legname* 96 (CAS, MO, W); Río Cochuna, Chicligasta, *Lillo* 1510 (GH), *O'Donnell* 10429 (BM, F, UC); Quebrada Caspinchango, *Lillo* 7340 (GH), *Venturi* 9598 (A, S); road to Tafi del Valle, Monteros, *Lourteig* 450 (A, U, US); Villa Nogués, above Tucumán, *Munz* 15469 (GH, NY, POM, US); from San Javier to Villa Nogués, *Ortiz in 1945* (A, BM, UC); Quebrada de Lules, *Quiroga* 7215 (F), *Venturi* 1295 (BM, CAS, F, GH, K, MO, RSA, UC, US, W), 2232 (A, POM, US, Z); Quebrada de Lules, Arroyo Grande, *Sleumer* 759 (B); Estancia Las Pavas, Dept. Chicligasta, *Venturi* 4657 (A, F, US). BRAZIL: Porto Alegre, cultivated, *Revicely in 1898* (W). CHILE: Jardín Suizo, Las Zorras, Valparaíso, cultivated, *Harshberger* 1046 (P, US); Prov. Concepción, cultivated, *Junge* 2975 (US).

Naturalized or cultivated specimens outside of South America: AZORES: Pico Island, above San Roque, *Brooke* 11337 (BM); Graciosa, Praia, Santana, *Gonçalves* 3113 (BM). COSTA RICA, ALAJUELA: Zarcuo, A. *Smith* 2775 (F). CARTAGO: Cartago, *Donnell Smith* 4804 (US). SAN JOSÉ: San José, *Pittier* 14104 (CM, GH, U, US). EL SALVADOR: Volcán de San Salvador, *Calderón* 2345 (F, US). GUATEMALA, SACATEPÉQUEZ: San Rafael, *Donnell Smith* 2176 (K, US); Antigua, *Standley* 62331 (F). SAN MARCOS: Volcán Tajumulco, *Johnston* 1231 (F), *Steyermark* 62331 (F). INDIA: Ootacamund, Nilgeri Hills, *Anstead* 122 (A), *Koelz* 11048 (NA), *Marcovicz in 1927* (LE); Kodaikanal, *Bembower* 9 (MO); Madras, Shembayanu, *Sauliers* 656 (A). JAMAICA: Cinchona Garden, Blue Mts., *Downes in 1926* (BM), *Harris* 7643 (G), *Sporne* 213 (CGE), ? 7605 (BM, F, K); vicinity of St. Helen's Gap, St. Andrew, *Maxon & Killip* 571 (A, F); near New Haven Gap, *Philipson* 914 (BM), *Roever* 4574 (MICH); Latimer River, *Seifriz in 1919* (BH). JAVA: Preanger, Pengalengan, *Hochreutiner* 1463 (G); Bandang, *Rauh* 13 (U). MEXICO, CHIAPAS: Piedracitos, Chamula, *Breedlove* 8018 (DS). DISTRITO FEDERAL: Villa Obregón, *Moore* 6395 (BH); Coyoacán, *Woronow* 2065 (LE). PUEBLA: Huauchinango, *Baldwin* 14390 (LL). VERACRUZ: Orizaba, *Botteri* 929 (GH, K, LE); Jalacingo, *Dodds* 57 (MO); Altotonga, *Foster in 1938* (BH, BM); Santa Ana Atzacana, N of Orizaba, *Rosas* 191 (MO); Santa Cruz, Altotonga, *Ventura* 1026 (CAS). PORTUGAL: Coimbra, *Rhodes* 37-64-126 (BH). RÉUNION: Forêt de Bébour, *Lorence & Cadet* 2423 (MO); Cilac, Réserve Matambu, *Lourteig* 2455 (MO), *Schlieben* 10966 (B, Z). SOVIET UNION: Leningrad Botanical Garden in 1843 (LE). SRI LANKA: Hadgala Garden, *Marcovicz in 1927* (LE). ST. HELENA: Longs, ridge above Sandy Bay, *Kerr* 107 (BM); Diana's Peak, *Salter* 38418 (BM). UNITES STATES, CALIFORNIA: Univ. Calif. Botanical Garden, Berkeley, *Hutchison* 49.802 (MO, RSA, UC, US); Los Angeles, *McClintock in 1942* (NA).

Unlike most species of sect. *Fuchsia*, which are often scandent with weak stems and branches, *Fuchsia boliviana* is sometimes arborescent and almost always self-supporting. Its most distinctive characters are the elongate, drooping racemes of usually scarlet flowers, the cylindrical ovaries and fruits, the fully

reflexed sepals after anthesis, and the early deciduous, ridged petals. In addition, this species generally has large, long petiolate, softly pubescent leaves that are opposite or ternate and sometimes alternate near the branch tips. It has been widely cultivated and naturalized in many countries of the world since the mid-1800s, but has long been confused in the literature with *F. corymbiflora*. The true *F. corymbiflora* has apparently never been cultivated and is a localized endemic in central Peru that has much finer pubescence than *F. boliviana*. It has strictly opposite, short-petiolate leaves, rounder ovaries, much shorter inflorescences, smooth, persistent petals, and non-reflexed sepals. *Fuchsia boliviana* is distinct and easily recognizable from other species of *Fuchsia*, but it is placed in a species group with *F. corymbiflora*, *F. mathewsii*, and *F. wurdackii* because of their large, pubescent, mostly opposite or ternate leaves and many-flowered racemes of long flowers with narrow petals. It also resembles *F. furfuracea* in the often ovate leaf shape, long petioles, similar floral dimensions, and dense pubescence.

As discussed in the section on reproductive biology, many populations of *F. boliviana* are largely autogamous. Populations from Venezuela and greenhouse-raised progeny from Bolivia both produced fully fertile fruits when isolated from pollinators. The unusually high degree of autogamy in this species is due to the close proximity of the stigma to the upper staminal whorl in many populations and to the loss or very slight degree of protogyny. The pattern of the latter stages of floral maturation is unique in *F. boliviana*. As the sepals split open and start spreading outwards at anthesis, the upper half of the petals begin to curve outwards. Within a day, the sepals become totally reflexed, and the petals attain their final, spreading-recurved posture. About two days after anthesis, the petals shrivel up and fall off, leaving the erect stamens and style along with the sepals reflexed back against the floral tube. The flowers remain on the plant for another day or two before the entire tube usually dehisces.

In addition to autogamy, vegetative reproduction is common in *F. boliviana*, occurring mostly by sucker growth or rooting from broken or cut stems. These two factors account to a large degree for the widely naturalized distribution of this species. The plants are prized for their very striking, numerous, red flowers in long, drooping racemes that can each last several months, and single seeds are sufficient to start extensive local populations in suitably cool, wet areas. In addition, *F. boliviana* has broader ecological tolerances than most species in the section and can survive short periods of drought and full sunlight.

The native range of *F. boliviana* appears to be centered in cloud forest on the eastern slopes of the Andes in southern Peru and Bolivia, possibly extending into northern Argentina. This conclusion is based on historical information as well as an analysis of the habitats and present-day distribution of the species. The only areas where *F. boliviana* can be said to form an integral part of relatively undisturbed tracts of forest is in southern Peru and Bolivia. Elsewhere, this species is found only close to towns, habitations, or heavily disturbed areas, as is typical of adventives or plants escaped from cultivation. Even in southern Peru, many collections are from cultivated or escaped plants. In Venezuela, the only populations of this species are found in the Cordillera de la Costa, where no other native *Fuchsia* occurs. Plants there grow mostly around the Colonia Tovar, an

old German agricultural colony that has received numerous introductions of plant material from travelers and from the numerous botanists who stayed there, such as Fendler, Moritz, and Pittier. *F. boliviana* is very commonly cultivated in the Sabana de Bogotá in Colombia and elsewhere throughout the mountains of that country, but it is always found near human habitations. The species is not known from Ecuador or northern Peru. In Jamaica, it occurs near old abandoned gardens such as Woodcutter's Gap and the Hill Garden at Cinchona and is undoubtedly naturalized (Adams, 1972 and pers. comm. to P. H. Raven).

According to Vargas (1964), *F. boliviana* was cultivated by the Incas and used as a motif in clay and wood artifacts. It continues to be cultivated today in the Cuzco area. The earliest cultivated plants of *F. boliviana* in Europe were grown from seeds brought from Cuzco, Peru. These seeds were collected by relatives of British nurseryman John Standish, who were traders and probably obtained the seed from garden plants there (Lindley, 1840). Progeny of these plants gave rise to many naturalized populations in other parts of the world. Seeds imported from Bolivia in 1873 were also grown in Europe and used to describe *F. boliviana*.

Several varieties or forms of *F. boliviana* have been described based on differences in floral tube length and degree of pubescence. *F. boliviana* var. *luxurians* was described by Johnston (1925) for plants with floral tubes 5–6 cm long from Venezuela, Central America, and Jamaica. In contrast, most plants from Argentina and Bolivia have much shorter floral tubes 3–4.5 cm long and shorter pubescence. The long-flowered populations generally have a more robust growth form and larger inflorescences. The leaves of the small-flowered Bolivian and Argentinian populations may be narrower in many cases than in naturalized plants, but considerable variation is found both in leaf and in floral tube dimensions. For example, *Kelley 1013* (CM, UC), from Sur Yungas, Bolivia, has some floral tubes 6 cm long and others only 4 cm long. Except for the smaller size of flowers and inflorescences in most southern populations, all of the characteristic floral and vegetative traits of these plants are identical to those of the more robust naturalized populations, and both kinds of plants are diploid.

In Dept. Cuzco, Peru, both robust, long-tubed plants as well as shorter-tubed plants are found. Plants such as *Balls B6715* (BM, K, NA, UC, US), cultivated in Paucartambo, near Cuzco, have floral tubes 5–6 cm long and closely resemble the naturalized populations in northern South America, Central America, and Jamaica. As discussed above, the earliest cultivated plants outside of Peru were from Cuzco, and illustrations in Lindley (1840) and Paxton (1841) appear to be from long-tubed plants. Since cultivation of this species in the Cuzco area dates back to the Incas, it is reasonable to suppose that robust, long-flowered plants were selected for cultivation by the local inhabitants, and these were later discovered by European visitors who sent seeds abroad to give rise to many of the naturalized populations known today. Due to the predominant autogamy of this species, populations with different floral tube lengths or with differences in the length and density of pubescence can easily be maintained. The only cultivated or naturalized populations with short floral tubes 4 cm long or less are from Portugal (*Rhodes 37-64-126*, BH) and some from India. Crosses between long-tubed plants from Colonia Tovar, Venezuela, and short-tubed plants from Dept.

La Paz, Bolivia, were made at Missouri Botanical Garden in 1979. These have given rise to normal, vigorous plants, with intermediate flower size.

A white-tubed variant of *F. boliviana* was described by Harrison (1849) as "*Fuchsia corymbiflora alba*." It has also been collected in Colombia (Berry 3552, COL, MO; Dept. Tolima) and is characterized by a total loss of red pigmentation in all parts of the plant except the petals. This might be due to a single mutation and is only known in cultivated or naturalized plants.

In summary, *F. boliviana* is a well demarcated species with populations that differ in floral tube length, robustness of the plant, and degree of pubescence. These differences can be explained, however, by a fairly wide and sometimes continuous variation within local populations, a long history of cultivation and probable selection of long-flowered forms, and a high degree of autogamy, which helps maintain small morphological differences. It is a very handsome species that is widely naturalized throughout the world in moist tropical and subtropical, montane habitats, but its probable native range extends from southern Peru (Dept. Apurimac of Cuzco) to Bolivia or northern Argentina. It is known to grow sympatrically with *F. sanctae-rosae* in Peru and Bolivia, but no hybrids between these two species have been detected.

50. ***Fuchsia corymbiflora*** Ruiz & Pavón, Fl. Peruv. Chil. 3:87, pl. 25, fig. a. 1802. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):551. 1941, pro parte. Munz, Proc. Calif. Acad. Sci. IV. 25:49, pl. 7, fig. 38. 1943, pro parte, non auct. pro *F. boliviana*. TYPE: Peru, Dept. Huánuco, woods of Chinchao and Muña, 1778–1788, *Hipólito Ruiz and José Pavón* (MA N°11/78, lectotype, here designated; photograph, MO).

Fuchsia velutina I. M. Johnston, Contr. Gray Herb. 75:36. 1925. TYPE: Peru, Dept. Huánuco, Yanano, ca. 2,000 m, 13–16 May 1923, *J. Francis Macbride* 3715 (F 535777, holotype; fragment, G; photographs, NY, POM, UC; GH, K, isotypes).

Fuchsia munzii J. F. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4):559. 1941. TYPE: Peru, Dept. Junín, Río Masamerich, 2,100–2,200 m, 1909–1914, *August Weberbauer* 6648 (F 628941, holotype; photographs, NY, UC; GH, UC, isotypes).

Scandent to erect shrubs 1–4 m tall. Young growth finely canescent to puberulent; older stems and leaves velutinous to subglabrous; branches few and spreading, branchlets terete, 2–3 mm thick, red to dull purple. Leaves opposite, very rarely ternate, firmly membranous, elliptic to oblong, acute at the base, acute to acuminate at the apex, 6–12(–19) cm long, 3–6(–9) cm wide, matte green above, pale green below; secondary veins 13–17 on either side of the midvein, sometimes reddish below; margin subentire to obscurely glandular-denticulate. Petioles 6–20(–30) mm long. Stipules triangular, 1–2 mm long, ca. 1.5 mm wide, sometimes connate, deciduous. Flowers few to many in terminal, corymbose, arching to drooping racemes or few-branched panicles; rachis 2–8 cm long; bracts lanceolate, 5–15 mm long. Pedicels pendant to ascending in fruit, 6–15 mm long. Ovary ellipsoid, 5–6 mm long, ca. 2 mm thick, puberulent. Floral tube narrowly funnelform, 40–65(–70) mm long, 2–2.5 mm wide and bulbous at the base, narrowed to 1.5–2 mm wide for ca. the basal 10 mm of the tube, then gradually widened above until 5–8 mm wide at the rim, minutely pubescent under a lens

to velutinous or strigillose outside, pubescent inside for most of length. Sepals lance-oblong, 12–15 mm long, 3.5–5 mm wide, acute at the apex, buds terete and slightly mucronate, spreading-divergent at anthesis. Tube and sepals pale pink to bright scarlet. Petals darker, red, oblong, acute to obtuse-tipped, 12–17 mm long, 4–5 mm wide, spreading and equal to or longer than the sepals at anthesis. Nectary shallowly 4-lobed, ca. 1.5 mm high. Filaments pink to red, 8–10 mm and 5–7 mm long; anthers oblong, 2.5–3 mm long, ca. 1.5 mm wide, white. Style pink, puberulent from the base to the rim of the tube; stigma capitate, 4-cleft at the apex, 2–2.5 mm long, ca. 2.5 mm wide, cream, exerted 3–6 mm beyond the anthers. Berry subglobose, $\pm$ tetragonous before maturity, 10–12 mm long, 8–10 mm thick, red; seeds reddish tan, 1.8–2.1 mm long, 1–1.4 mm wide. Gametic chromosome number $n = 11$.

Distribution: Endemic to cloud forest on the eastern slopes of the central Peruvian Andes in Depts. Huánuco, Junín, and Huancavelica; (1,500–)2,250–2,850 m (Fig. 63).

Representative specimens examined: PERU, HUANCAMELICA: without locality, *Weberbauer* 6565 (F, GH). HUÁNUCO: near Pano, above La Molina, *Asplund* 13699 (RSA); 5 km W of Carpish tunnel, *Berry & Aronson* 3082 (MO, USM); Carpish, *Ferreira* 1828 (MO, USM); Carpish, above Acomayo, *Hutchison et al.* 5919 (F, MO, NY, RSA, UC, US, USM); Huacachi, near Muña, *Macbride* 4180 (F, G); road from Mirador to Chinchao, *Mexia* 7765 (GH, K, MO, UC, US); Muña, *Pearce* 148 (K), 512 (BM, K). JUNÍN: 55 km above and W of Satipo on road to Concepción, *Berry & Aronson* 3079 (MO, USM); San Juan to Huacapistana, *Ferreira* 11293 (USM); above Huacapistana, *Sandeman* 95 (BM, K); Km 170 Satipo-Concepción, *Seibert* 2384 (MO, POM, US). WITHOUT LOCALITY: *Ruiz & Pavón* (BM, F, MA, MO).

This species can be recognized by its normally soft, velutinous, opposite leaves and terminal racemes of slender flowers with short pedicels and round fruits. These characters place it in the *Fuchsia boliviana* species group, where it is possibly most closely related to *F. wurdackii* from northern Peru. For over a century its name was used for the species later described as *F. boliviana*, a commonly cultivated and naturalized, ornamental plant from southern Peru and Bolivia that has cylindrical fruits, flowers with reflexed sepals and much longer racemes. Munz (1943) also included *F. dependens* under this species, but it is distinct and restricted to northern Ecuador and southern Colombia and has quaternate, longer petiolate leaves with more toothed margins.

Plants from the southern part of the range in Junín have been called *Fuchsia munzii*. They have much paler pink flowers than populations from Huánuco, and their leaves are lighter green with wine purple veins. This appears to be due to the loss of some of the dark red pigmentation in the plant. Although the Junín plants are often nearly glabrous, the characteristic fine, erect hairs of *F. corymbiflora* can usually be seen upon careful examination. They also have the same 4-sulcate, rounded fruits and finely pilose styles as *F. corymbiflora*. In the Carpish area, considerable variation in leaf width occurs.

Fuchsia corymbiflora is sympatric with *F. abrupta*, *F. ceracea*, *F. decussata*, and *F. denticulata*. *Fuchsia abrupta* is a long-tubed species with opposite leaves that can be confused with *F. corymbiflora* in dried specimens, but it can be distinguished by its cylindrical fruits, divergent pedicels, often hispid pubescence, and strongly divergent sepals and petals.

51. *Fuchsia wurdackii* Munz, Brittonia 16:229. 1964. TYPE: Peru, Dept. Amazonas, Prov. Chachapoyas, Quebrada Molino, 5 km below Chachapoyas, 2,200 m, 30 May 1962, *John J. Wurdack* 622 (US 2404206, holotype; photograph, MO).

Erect shrubs 1–1.5 m tall. Young growth finely pilose, older stems pilose and dull tan, 3–10 mm thick. Leaves opposite or ternate, softly membranous, narrowly elliptic-ovate, acute to subacuminate at both ends, 7–18 cm long, 2–8 cm wide, shortly soft pilose on both sides; secondary veins 7–14 on either side of the midvein; margin subdenticulate. Petioles pilose, 7–43 mm long. Stipules conspicuous, lanceolate, usually with an obtuse apex, pale membranous, 3–5 mm long, 0.5–2 mm wide, sometimes connate, usually persistent and reflexed. Flowers few to many in terminal, corymbose, drooping racemes; rachis 4–18 cm long; bracts lance-linear, denticulate, 15–50 mm long, 3–8 mm wide. Pedicels 9–11(–25) mm long. Ovary oblong, 7–10 mm long, 3–4 mm thick. Floral tube narrowly funnel-form, 31–50 mm long, 2–3 mm wide and slightly bulbous at the base, gradually widened above until 5–8 mm wide at the rim, pilose to short villous outside, pilose inside in lower $\frac{2}{3}$. Sepals oblong, obtuse, 9–16 mm long, 3–5 mm wide, spreading at anthesis. Tube and sepals coral red. Petals red, oblong to broadly elliptic, obtuse at the apex, 11–20 mm long, 4–8 mm wide. Nectary unlobed or shallowly 4-lobed, ca. 1.5 mm high. Filaments red, 5–9 mm and 3–6 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide, white. Style red, glabrous; stigma capitate, shortly 4-lobed at the apex, 2–3 mm long, 2–4 mm wide, pink, exserted 1–3 mm beyond the anthers. Berry cylindric to ellipsoid, 17–20 mm long, 9–11 mm thick; seeds 1.6–2 mm long, 0.9–1.2 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Endemic to moist sites on slopes leading into the Río Utcubamba valley in Dept. Amazonas; 2,100–2,400 m (Fig. 63).

Representative specimens examined: PERU, AMAZONAS: 9 km above Leimebamba on road to Balsas, *Berry & Escobar* 3616 (MO, USM); Leimebamba-La Joya trail, *Boeke* 1786 (MO); Cerros Calla-Calla, at San Miguel, 5 km above Leimebamba, *Hutchison & Bennett* 4542 (UC, USM), *Hutchison & Wright* 4884 (UC); vicinity of Leimebamba, upstream along creek leading into Río Utcubamba, *Hutchison & Wright* 4888 (F, MICH, MO, NY, RSA, UC, US, USM); Cerro Puma Urco, SE of Chachapoyas, *Soukup* 4097 (US).

This is a long-tubed, racemosely flowered species that is distinctive in its obtuse petals and sepals, pilose pubescence, and large, pale stipules. Its rather long inflorescences with narrow bracts are similar to those of *Fuchsia pilosa*, but that species has much smaller flowers and coarser pubescence. *Fuchsia wurdackii* shares many features with *F. boliviana* including the large, pubescent, long-petiolate leaves and lanceolate bracts, but lacks the acute, reflexed sepals and long, cylindrical fruits of that species. Its closest relative is probably *F. corymbiflora*, known from central Peru, which has similar flowers and short, soft pubescence, but shorter fruits and petioles. Since *F. wurdackii* is the lowest-altitude species in northern Peru, it does not occur sympatrically with any other species of the section, although both *F. fontinalis* and *F. mathewsii* occur nearby (Fig. 10).

52. *Fuchsia mathewsii* J. F. Macbride, *Candollea* 8:24. 1940; *Field Mus. Nat. Hist., Bot. Ser.* 13(4):558. 1941. Munz, *Proc. Calif. Acad. Sci.* IV. 25:44. 1943. TYPE: Peru, Dept. Amazonas, Chachapoyas, 1830–1841, *Andrew Mathews* (G-BOIS, holotype; photograph, MO; G-DEL, isotype).

Fuchsia fischeri J. F. Macbride, *Field Mus. Nat. Hist., Bot. Ser.* 13(4):554. 1941. Munz, *Proc. Calif. Acad. Sci.* IV. 25:45. 1943. TYPE: Peru, Dept. Cajamarca, Prov. Hualgayoc, Chugar, 2,700–2,900 m, 1906, *August Weberbauer 4097* (G, holotype).

Fuchsia storkii Munz, *Proc. Calif. Acad. Sci.* IV. 25:37, pl. 6, fig. 33. 1943. TYPE: Peru, Dept. Cajamarca, Prov. Chota, pass S of Conchán, 2,500 m, *Harvey E. Stork & Ovid B. Horton 10073* (F 1052248, holotype; photograph, NY; K, UC, isotypes).

Suberect shrubs 1–3 m tall, puberulent to mostly densely pilose with white to generally rusty hairs. Branchlets triangular (when leaves are ternate) or rarely subtetragonous, dull purple to ferrugineous-pilose; older branches 7–14 mm thick, with pilose, reddish bark exfoliating in strips. Leaves mostly ternate, occasionally quaternate, firmly membranous, narrowly elliptic to oblanceolate or elliptic, at times slightly asymmetrical and curved to one side, narrowly obtuse at the base, acute at the apex, 4–16 cm long, 1.2–5 cm wide, dull to subnitid dark green and pilose to strigose above, lighter green and mostly rusty-pilose below, with hairs denser along the nerves, blades sometimes purple flushed; secondary veins 8–12 on either side of the midvein; margin subdenticulate. Petioles pubescent to densely ferrugineous-pilose, 3–10(–25) mm long. Stipules narrowly lanceolate when young, becoming thick and triangular with age, dark, 2–3 mm long, ca. 1 mm wide, subpersistent. Flowers numerous and crowded at the tips of terminal, arching-drooping racemes or few-branched panicles; rachis 3–6 cm long; bracts lacking or rapidly deciduous, 10–25 mm long, ca. 6 mm wide. Pedicels pubescent to pilose, 12–25 mm long. Ovary ellipsoid, 5–7 mm long, 2–3.5 mm thick, green to purple. Floral tube narrowly funnelform, (32–)36–63 mm long, 2.5–3.5 mm wide and slightly bulbous at the base, narrowed to ca. 2 mm wide above the nectary, then widened gradually above until 5–8 mm wide at the rim, mostly pilose outside, pilose to villous inside in lower $\frac{1}{2}$. Sepals lanceolate, blunt tipped and broader than the tube in bud, 11–16 mm long, 4–5 mm wide, lobes often splitting open in the middle before detaching at the tips, suberect to spreading at anthesis. Tube and sepals pale pink to lavender or light red. Petals slightly darker than the tube or sepals, crimson to light purple, lanceolate to narrowly elliptic, 10–16 mm long, 3–4 mm wide, obtuse to subacuminate at the apex, spreading at anthesis. Nectary unlobed, ca. 1.5 mm high. Filaments dull white to light red, 7–9 mm and 4–6 mm long; anthers oblong, 2–2.5 mm long, ca. 1.5 mm wide, white. Style pink, villous from the base to the rim of the tube; stigma subglobose, 4-cleft at the apex, 2.5–3.5 mm long, 2–3 mm wide, pink. Berry subglobose to ellipsoid, 10–16(–20) mm long, 8–11(–15) mm thick, lustrous red purple; seeds 1.8–2.1 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Northern Peru. Scattered to locally frequent shrubs in cloud forest along streamsides or in semidisturbed sites such as roadbanks or thickets, or in somewhat drier, shrubby woodlands; Depts. Cajamarca and Amazonas; (2,500–)2,700–3,350 m (Fig. 63).

Representative specimens examined: PERU, AMAZONAS: 42 km E of Balsas on road to Leimebamba, *Berry & Escobar* 3603 (MO, USM); 51 km E of Balsas on road to Leimebamba, *Berry & Escobar* 3606 (MO); 24 km above Leimebamba on road to Balsas, *Berry & Escobar* 3612 (MO); Prov. Chachapoyas, *Mathews* 2112 (K), *s.n.* (BM, K, OXF); above Colcamar, *Pennell* 15620 (PH). CAJAMARCA: 39 km W of Celendín on road to Cajamarca, *Berry & Escobar* 3602 (MO, USM); canyon of Río Marañón above Balsas, 5 km below summit of road to Celendín, *Hutchison & Wright* 5356 (F, NY, RSA, UC, USM); E of Cordillera de Cumulloa to Celendín, *Pennell* 15158 (PH, USM).

The generally rusty-pilose pubescence, mostly oblanceolate, ternate, short-petiolate leaves, and the short, nodding inflorescences of long-tubed, pinkish flowers characterize this species. It is somewhat intermediate between the *Fuchsia boliviana* and the *F. dependens* species groups and apparently has no close relative, but it is placed in the former group because of the mostly racemose flowers and generally ternate leaves. *Fuchsia mathewsii* is quite common on the Cerros de Calla-Calla in Dept. Amazonas, occurring on both the western slopes above the dry Marañón valley and on the moister, eastern slopes. Considerable variation in the length and redness of pubescence exists within these populations, and the plants on the western side tend to have somewhat longer petioles than those on the eastern, Leimebamba side. There is just a short distance, ca. 20 km by air, between the populations on the east side of the arid Río Marañón valley in Dept. Amazonas and those on the opposite slopes in Dept. Cajamarca, and the differences between them are no greater than the variation found locally on the Amazonas side. The two species described from areas farther north in Cajamarca, *F. fischeri* and *F. storkii*, show no significant differentiation from the populations described above. *Fuchsia storkii* is supposedly distinguished by its short (30 mm long) flowers, but the type at F examined by Munz proves to have only young flowers; fully extended flowers on the isotype at K have floral tubes up to 48 mm long, well within the normal range for *F. mathewsii*.

Fuchsia fontinalis often has rusty-pilose pubescence and paniculate inflorescences like *F. mathewsii*, but the rachis is more extended and the flowers shorter. Whereas *F. mathewsii* occurs on both sides of the north-south running Cerros de Calla-Calla (between the Marañón and Utcubamba river valleys), *F. fontinalis* grows only on the eastern slopes. There, the two species are sympatric between 3,200 and 3,300 m, at the lower altitudinal limit of *F. fontinalis* and the upper limit of *F. mathewsii* (Fig. 10). They were found growing together in low woods along a pasture border, and a probable hybrid between them was collected growing out of a stone wall nearby (*Berry & Escobar* 3613, MO, USM: 3,260 m, 15 July 1979). This individual has intermediate floral tube lengths (22–32 mm), short, but bracteate inflorescences, and reduced pollen stainability of 36.6% of 500 grains. Another possible hybrid or backcross to *F. mathewsii* is *Berry & Escobar* 3611 (MO), found 1 km above 3613; it is much closer to *F. mathewsii*, with floral tubes ca. 36 mm long, but the style is glabrous, and the inflorescence is bracteate and nearly 12 cm long, as in *F. fontinalis*. Its pollen stainability is also low, 46.6% of 500 grains.

53. *Fuchsia dependens* Hooker, Ic. Pl. t. 65. 1837. TYPE: Ecuador, Prov. Pichincha, woods on W side of Volcán Pichincha, 1838, *William Jameson* 81 (K, holotype; photograph, MO).

Fuchsia corymbiflora sensu J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):551. 1941, pro parte; sensu Munz, Proc. Calif. Acad. Sci. IV. 25:49. 1943, pro parte; Opera Bot., Ser. B, 3:13. 1974, pro parte.

Erect to usually scandent-climbing shrubs 2–10 m high, with arching to hanging branches 0.5–3 m long. Branchlets canescent, dull red, 2–8 mm thick, with tan bark exfoliating in longitudinal strips. Leaves mostly quaternate, rarely in whorls of 3 or 5, membranous, narrowly elliptic to ovate, acute at both ends, 5–14(–15) cm long, 2–5(–6) cm wide, dull green and strigillose above, incanous and paler below, especially when dry; secondary veins 11–14(–16) on either side of the midvein, $\pm$ impressed above and prominent below, midrib reddish; margin usually undulate and conspicuously glandular-denticulate. Petioles puberulent, reddish, $\frac{1}{5}$ – $\frac{1}{3}$ the length of the blade, 14–35 mm long. Stipules lanceolate, 1.5–2 mm long, 0.4–0.5 mm wide, deciduous. Flowers numerous in dense, drooping, terminal panicles or series of terminal and subterminal, corymbiform racemes; rachis 2–6 cm long when young, 8–25 cm long in fruit; bracts elliptic, 5–20 mm long, 3–10 mm wide, short-petiolate, sometimes reflexed. Pedicels slender, pendant, incanous, 5–10 mm long. Ovary ellipsoid, 5–7 mm long, 2–3 mm thick. Floral tube narrowly funnelform or subcylindric, 40–50 mm long, 3–4 mm wide and nodose at the base, narrowed to 2.5–3 mm wide in basal $\frac{1}{4}$, then gradually widened above until 5–8 mm wide at the rim, puberulent outside, densely pilose inside in the narrowed part of the tube. Sepals lance-oblong, 12–13 mm long, 4–5 mm wide, obtuse to shortly acute-tipped, spreading at anthesis. Tube orange red to scarlet, sepals same but with dull green tips. Petals orange red, narrowly lanceolate, 12–14 mm long, 3–4 mm wide, acute at the apex, spreading to $\pm$ recurved at anthesis. Nectary irregularly 4-lobed, 1–2 mm high. Filaments red, 9–11 mm and 5–7 mm long; anthers oblong, 2.5–3 mm long, 1.5–2 mm wide, cream. Style totally glabrous, light red; stigma capitate to subobconic, slightly 4-parted at the apex, 2–2.5 mm long, 1.5–2 mm wide, dull pink, exserted 3–10 mm beyond the anthers. Berry ellipsoid, puberulent, 12–16 mm long, 7–12 mm thick; seeds tan brown, 1–1.2 mm long, ca. 0.6 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Colombia to central Ecuador. In cloud forest on the west slopes of the Cordillera Occidental of the Northern Andes from Carchi to Pichincha and on the east slopes of the Cordillera Central in Imbabura and Carchi; also in the drier Central Valley of Ecuador from Pichincha to Carchi and in the Nudo de Pasto area in Nariño, Colombia, occurring commonly in hedgerows; 2,400–3,300 m (Fig. 66).

Representative specimens examined: COLOMBIA, NARIÑO: between pasto and Río Bobo, *Barclay* 4645 (COL); 8 km S of Pasto towards Ipiales, *Berry* 3145 (MO); Oscurana, S slopes of Volcán Gualcalá, 14 km from Piedrancha, *Fosberg* 21186 (RSA, US); Laguna La Cocha, Páramo el Tábano, *García-Barriga* 7822 (COL, US); Volcán Galeras, near Pasto, *Lehmann* 5497 (F, GH, K, S, US); road from Cuatro Esquinas to Quitasol, *Mora* 290 (COL); region of Pedregal, S of Yacuanquer, *Schultes & Villarreal* 7898 (COL, RSA); base of Volcán Galeras, above Obonuco, *Schultes & Villarreal* 8042 (COL, GH, RSA). ECUADOR, CARCHI: between Paja Blanca and El Cucho, *Acosta Solis* 10476 (F); Guaca, San Gabriel, *Balls* 7344 (BM, K, MO, NA, UC, US); El Angel, *Berry & Berry* 2560 (MO); 38 km W of Tufiño on road to Maldonado, *Berry* 3148 (MO); ca. 4 km W of El Carmelo, *Berry* 3164 (MO, QCA); town of J. Andrade, on Panamerican highway, *Berry* 3166 (MO, QCA).

IMBABURA: Rosaspampa, E slopes of Volcán Mojanda, *Acosta Solis* 8089 (F); 4–5 km W of Otavalo to Laguna de Mojanda, *Berry & Berry* 2552 (MO), *Berry* 3172 (MO, QCA); Mojanda, ca. 10 km SSW of Otavalo, *Sparre* 13480 (S). PICHINCHA: San José de Minas, *Benoist* 3961 (P); 19 km W of Cotacollao on road to Nanegal, *Berry & Escobar* 3176 (MO, QCA); 10 km E of Cayambe, *Harling* 4343 (NY, S); between Calacati and Nono, *Hartweg* 986 (BREM, CGE, G, K, LE, NY, OXF, P, W); Hacienda Yunguilla, NW of Calacati, *Haught* 3170 (A, BH, U); Pululahua Crater, ca. 22 km N of Quito, *Humbles* 6281 (AAU, NY); between Cotacollao and Nono, *Mexia* 7658 (BM, GH, K, MO, NY, POM, S, U, UC, US); Volcán Pichincha, *Spruce* 5471 (BM, CGE, G, K, NY, OXF, TCD, W).

This species is part of a group with mostly quaternate leaves and paniculate inflorescences. Both Munz (1943) and Macbride (1941) treated this species under *Fuchsia corymbiflora*, but that is a distinct species from central Peru with entirely opposite leaves and usually racemose inflorescences. *Fuchsia dependens* is closely related to *F. hartwegii*, with shorter flowers, and to *F. hirtella*, which has more entire leaves with short petioles. Both these species occur north of the range of *F. dependens* in Colombia. It is further distinguished by its densely cinereous pubescence and long-petiolate leaves with conspicuously denticulate and sometimes undulate margins.

Fuchsia dependens has wide ecological tolerances for sect. *Fuchsia*. On the eastern slopes of the Cordillera Central in Ecuador and on the western slopes of the Cordillera Occidental, it is found in cloud forest and occurs mostly as a climber or scrambling shrub. It also occurs in the drier Central Valley of Ecuador and in the Nudo de Pasto in southern Colombia, where it grows more compactly and often as upright shrubs in hedgerows. This is an excellent example of this upland area being used as a migration corridor for a species to spread from one structural unit of the Andes to another. Other species that occur sympatrically with *F. dependens* are *F. ampliata*, *F. corollata*, and *F. sessilifolia*, but no hybrids were detected with them.

- 54. *Fuchsia hirtella*** Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 6:107. 1823. Munz, Proc. Calif. Acad. Sci. IV. 25:47, pl. 7, fig. 36. 1943. TYPE: Colombia, Dept. Cundinamarca, in mountains near Fusagasugá, ca. 1,900 m, July–Sept. 1801, *Alexander von Humboldt & Aimé Bonpland* (P, holotype; photograph, F; microfiche, MO). *Bonpland* 1783 at P is a possible isotype.

Climbing-scandent to suberect shrubs 2–5 m tall. Branchlets subterete, 2–4 mm thick, green to reddish and densely hirtellous; older branches 10–25 mm thick, with freely exfoliating bark. Leaves mostly quaternate, occasionally in whorls of 3 or 5, membranous, elliptic to narrowly elliptic or obovate, acute to truncate at the base, acute at the apex, 6–13 cm long, 1.8–5 cm wide, subnitid dark green and loosely strigose above, pale green and densely strigose below; secondary veins 10–15 on either side of the midvein, prominent below; margin entire to subdenticulate. Petioles strigose, reddish, 3–8(–15) mm long. Stipules lance-linear, hirtellous, 1.5–2 mm long, ca. 0.5 mm wide, deciduous. Inflorescence an arching to pendant panicle at the tips of branches; flowers numerous, subtended by reduced, sometimes reflexed leaves; rachis hirtellous, 4–20 cm long. Pedicels slender, pubescent, 4–12 mm long. Ovary cylindric, 5–7 mm long, ca. 2 mm thick. Floral tube subcylindric, 34–40 mm long, 3–4 mm wide and bulbous at the base, narrowed to 2–3 mm wide in the basal $\frac{1}{3}$, then gradually widened above until 5–9 mm wide at the rim, strigillose to pilose outside, densely villous

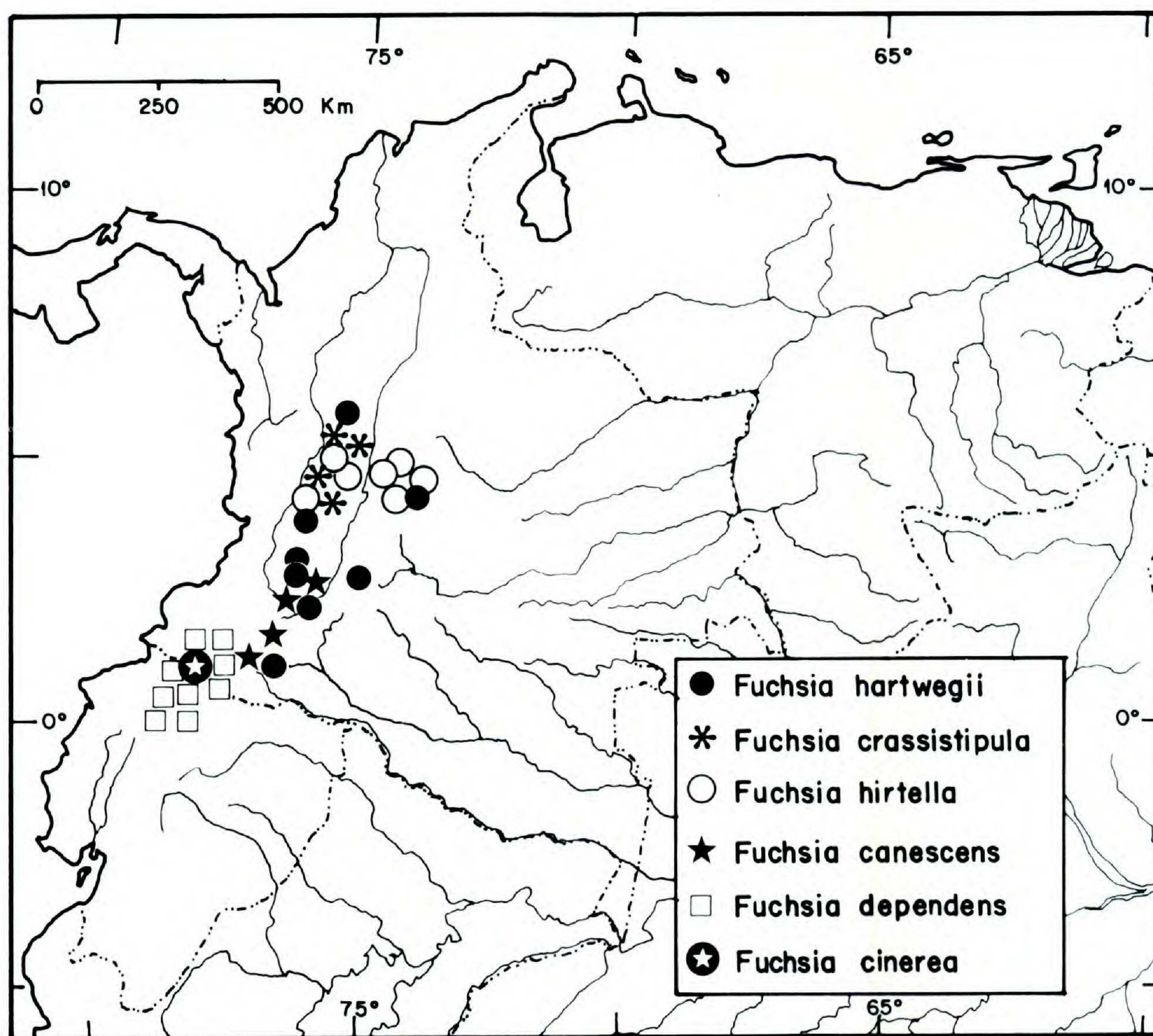


FIGURE 66. Distribution of the *Fuchsia dependens* species group.

inside in basal $\frac{1}{2}$. Sepals lanceolate, acuminate, 12–16 mm long, 3–4 mm wide, long-tapered to apiculate in bud, spreading to divergent at anthesis. Tube and sepals subnitid lavender to reddish pink. Petals somewhat darker, crimson, narrowly elliptic-oblong, sharply acute at the apex, 12–16 mm long, 3–4 mm wide, spreading at anthesis. Nectary unlobed, light green, ca. 1.5 mm high and ca. 1 mm thick. Filaments pink, 8–14 mm and 5–10 mm long; anthers oblong, 2.5–3 mm long, 1.5–2 mm wide, dull white. Style slender, glabrous, pink; stigma globose to subobconic, 4-parted apically, 2–2.5 mm long, ca. 2 mm wide, pale pink to dull red, exserted 3–9 mm beyond the anthers. Berry cylindric-ellipsoid, 14–18 mm long, 8–9 mm thick; seeds 1.4–1.7 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia. In the Cordillera Oriental in Cundinamarca, mostly on the outer slopes of the Sabana de Bogotá; in the Cordillera Central from Caldas to Valle; growing in moist cloud forest clearings or thickets between 2,500 and 3,300 m (Fig. 66).

Representative specimens examined: COLOMBIA, CUNDINAMARCA: San Miguel, Km 35–36 S of Sibaté to Fusagasugá, *Barclay et al.* 3403 (COL, US), *Berry* 3543 (COL, MO); Páramo de Sumapaz, near

Lagunitas, ca. 5 km SSW of San Juan, *Cleef* 8451 (COL, MO, U, US); Boca de Monte, *Cuatrecasas et al.* 25856 (COL); San Miguel, *Cuatrecasas & Jaramillo* 12011 (BH, COL, F, US); Fómeque, between Lago de Chingaza and Cerro Verde, *García-Barriga* 17676 (COL); Zipaquirá-Pacho highway, *Haught* 5977 (COL, NY, POM, US); La Vega, road to Facatativá, Río Sabaneta, *Schneider* 1206 (COL, S); Bojacá, *Schneider* 1263 (S); Zipacón, below Boca de Monte, *Uribe-Uribe & Villarreal* 2560 (COL, US); 14 km S of Mosquera to La Mesa, *Uribe-Uribe* 5929 (COL, US). QUINDÍO: 12 km from Salento towards Cocora, along Río Quindío, *Escobar* 1016 (MO); Amarguras, above Salento towards Romerales, *Hawkes* 418 (COL, K, US); Laguneta to Magaña, old Quindío trail, *Killip & Hazen* 9418 (GH, NY, PH, US). RISARALDA: Guayabal, watershed of the Río Otún, below El Bosque, *Cuatrecasas* 23306 (F, RSA, VALLE). TOLIMA: Mediación, *André* 2152 (K, NY); 3 km E of La Línea, between Giradot and Armenia, *Berry* 3144 (MO); between El Líbano and Murillo, *García-Barriga* 12274 (COL, US); La Lora to Cucarronera, new Quindío trail, *Hazen* 9679 (GH); Volcancitos, *Holton* 893 (K, NY, PH); Tohecito, *Triana* 3809 (G, US).

This species is closely allied to *Fuchsia hartwegii* and *F. dependens*, which share a similar paniculate inflorescence and quaternate, pubescent leaves. It can be distinguished from these, however, by its subsessile or shortly petiolate leaves, hirtellous pubescence, and pinkish flowers. Its flowers are longer than those of *F. hartwegii*, which it apparently overlaps in range in the Cordillera Central.

This is a relatively high elevation cloud forest species and is common along the moist, outer slopes of the Sabana de Bogotá. As with *Fuchsia venusta* and *F. petiolaris*, it also grows adjacent to Cundinamarca in Tolima, in the Cordillera Central, where it probably spread secondarily. At its lower altitudinal limit, *F. hirtella* is sympatric with *F. venusta* and *F. verrucosa*. Probable hybrids with *F. venusta* were found between 2,500 and 2,600 m on the southeastern edge of the Sabana de Bogotá in Cundinamarca, where both species are locally common and grow in identical habitats. Table 17 shows the intermediate morphological characters of the two putative hybrids collected. Pollen stainability of these plants was reduced by 18 to 28% relative to their presumed parents (see Table 18). Normal pairing of 11 bivalents was found in meiotic preparations of *Berry* 3547 (COL, MO), but occasional chromosomal bridges and fragments were observed at anaphase I.

- 55. *Fuchsia hartwegii* Benth**am, Pl. Hartw. 179. 1845. Munz, Proc. Calif. Acad. Sci. IV. 25:63, pl. 9, fig. 53. 1943. TYPE: Colombia, Dept. Cauca, in woods near Pitayo and Huambía, common in hedgerows at Huambía, 1841–1843, *Theodor Hartweg* 994 (K Benth. Herb., holotype; photograph, MO; BM, BR, BREM, CGE, G, K Hooker Herb., LE, OXF, P, W, isotypes).

Low shrubs or small trees 0.5–4 m tall or scandent-climbing in thickets or trees to 8 m above the ground. Young growth usually canescent; branchlets 2–4 mm thick, subterete, reddish, hirtellous to strigose; older branches erect or arching-flexuous on scandent bushes, 0.5–3 m long, 8–50 mm thick, with tan gray, flaking bark. Leaves mostly quaternate, occasionally up to 7 per whorl, firmly membranous, narrowly to rather broadly elliptic or oblanceolate, acute to attenuate at the base, acute to acuminate at the apex, 3–15.5 cm long, 1.5–5.5 cm wide, subnitid dark green and strigose to subglabrous above, pale green and hirtellous to strigose below, especially along the veins; secondary veins 8–14 on either side of the midvein, impressed above, prominent and reddish below; margin glandular-denticulate. Petioles hirtellous to strigose, 5–32 mm long. Stipules lanceolate, thick at the base, filiform at the tip, 1–2 mm long, ca. 0.6 mm wide,

TABLE 17. Comparison of morphological characters of *Fuchsia hirtella*, *F. venusta*, and presumed hybrids.

	<i>F. hirtella</i> (Berry 3543)	Hybrid (Berry 3546)	Hybrid (Berry 3547)	<i>F. venusta</i> (Berry 3544-C, 3547)
Stem color	Green to pink	Wine red	Wine red	Wine red
Stem pubescence	Hirtellous	Canescent	Canescent	Puberulent
Number of leaves/whorl	4	3–4	3–4	3
Leaf surface	Matte	Subnitid	Subnitid	Nitid
Leaf pubescence	Strigose both sides	Strigose below	Strigose on veins below	Glabrous both sides
Inflorescence type	Paniculate	Subpaniculate	Racemose	Subracemose
Rachis length	13 cm	10–11 cm	5–8 cm	3–4 cm
Pedicel length	9–12 mm	10–25 mm	8–22 mm	16–30 mm
Floral tube length	35–36 mm	35–38 mm	45 mm	30–37 mm
Floral tube color	Pink	Pink purple	Pink purple	Dull orange
Sepal length	12–15 mm	15–18 mm	19 mm	16–20 mm
Sepal angle at an- thesis (approx.)	30°	30°	90°	90°
Petal length	12–14 mm	11–14 mm	22–23 mm	16–20 mm
Petal surface	Smooth	Smooth	Undulate	Undulate
Petal color	Pink	Red purple	Red purple	Orange red

deciduous. Flowers hermaphroditic or gynodioecious, numerous, fasciculate, racemose, or more commonly paniculate at the branch tips; rachis 5–20 cm long; bracts broadly ovate, sometimes sessile, 6–20 mm long, 3–15 mm wide. Pedicels slender, arching to pendant, pubescent, 4–12 mm long. Ovary ellipsoid, strigose to pilose, 3.5–5 mm long, 1.5–2 mm thick. Floral tube narrowly funnelform, 13–20(–24) mm long, 1.5–3 mm wide and bulbous at the base, constricted to 1–2 mm wide above the nectary and gradually widened above until 2–5 mm wide at the rim, strigose to pilose outside, densely villous inside in the lower ½–⅓. Sepals lanceolate, 7–12 mm long, 2.5–4 mm wide, acute at the apex, forming a short tip in bud, spreading at anthesis. Tube and sepals subnitid orange red to bright crimson. Petals red, very narrowly elliptic, 5–9 mm long, 1.5–3 mm wide, narrowly acute at the apex. Nectary green, unlobed, 1.5–2 mm high, ca. 0.8 mm thick. Filaments red, 5–8 mm and 3–5 mm long; fertile anthers oblong, 1.5–2 mm long, 0.7–1 mm wide, white, abortive ones ca. ½ as large and nondehiscing. Style glabrous, red; stigma subglobose, barely 4-parted at the apex, 1–1.5 mm long, 1–1.5 mm wide, pale red, exserted 3–6 mm beyond the anthers. Berry globose when ripe, 6–9 mm long, 5–8 mm thick, nitid purple red; seeds tan to reddish brown, 1.1–1.3 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 11$.

Distribution: Colombia. Most common in the Cordillera Central from southern Valle to Putumayo, as a scandent or hedgerow shrub in cloud forest between 2,350 and 2,750 m; present farther north in the Cordillera Central around 3,000 m in Caldas, Tolima, and southern Antioquia; a few collections are known from the Cordillera Oriental in Huila and Cundinamarca at 2,100–2,300 m (Fig. 66).

TABLE 18. Pollen stainability of *Fuchsia hirtella*, *F. venusta*, and presumed hybrids.

Collection	Stainable Pollen Grains (% of 500)
<i>Berry 3543 (F. hirtella)</i>	95.6%
<i>Berry 3546 (hybrid)</i>	78.4%
<i>Berry 3547 (hybrid)</i>	68.8%
<i>Berry 3544-C (F. venusta)</i>	96.2%

Representative specimens examined: COLOMBIA, ANTIOQUIA: Páramo de Sonsón, *Guarín 3479* (COL, US). CALDAS: without locality, *Dawe 741* (K, NY, US); 7 km N of Manizales, *Escobar 1002* (MO); Manizales, *Sandeman 5666* (COL, K, OXF); San Félix, near Salamina, *Tómas 2406* (BH). CAUCA: Puracé, *Alston 8137* (BM, RSA, UC); between Silvia and Totoró, *Berry 3573* (COL, MO); 21 km above Piendamó on road to Silvia, *Berry 3572* (COL, MO); Quebrada Santo Domingo, headwaters of the Río Palo, *Cuatrecasas 19159* (A, BH, COL, VALLE); La Tolda, above Tacueyo, watershed of Río Palo, *Cuatrecasas 19421* (A, BH, VALLE); Puracé, 17 km SE of Popayán, *Fosberg 20303* (COL, RSA, S, US); Río Santo Domingo, 20 km SE of Corinto, *Fosberg 21306* (GH, RSA, S, US); from Puracé to Alto de San Rafael, *García-Barriga & Hawkes 12856* (COL, US); Paispamba, *Haught 5302* (COL, US); Cococnuco, *Killip 6829* (GH, NY, PH, US); Central Andes of Popayán, *Lehmann 5613* (F, K); Páramo de Guanacas, *Lehmann 5614A* (F, GH, K, PH, S, US); Alto de Pesares, *Lehmann 5614B* (F, K); Páramo de Puracé, at Chiquín, *Pérez-Arbelaez & Cuatrecasas 5973* (COL, F, US); between Popayán and Puracé, bridge at Uarló, *Pérez-Arbelaez & Cuatrecasas 5880* (COL, F); headwaters of Río Lopez, Río Palo basin, Tierra Adentro, *Pittier 1068* (US); Prov. of Popayán, *Triana s.n.* (BM); Silvia, Guambía, *Yepes-Agredo 3088* (COL). CUNDINAMARCA: Fómeque, *Dawe 352* (K, US); Río Blanco valley, 6 km W of Gutiérrez, *Grant 9695* (RSA, US); between Guayabetal and Quétame, *Vogel 175* (U). HUILA: ca. 75 km W of La Plata on road to Puracé, *Berry 3591* (COL, MO); headwaters of Río Fortalecillas, just below Paso de Las Cruces, 39 km E of Neiva, *Fosberg 19785* (NY, RSA, S, UC, US); Balsillas, on Río Balsillas, *Rusby & Pennell 789* (NY, US), *810* (NY). META: Río Grande, S of Cordillera de Las Cruces, *Fosberg 20872* (US). PUTUMAYO: above Sibundoy on road to La Cocha, *Berry 3255* (MO, PSO); Balsayaco, valley of Sibundoy, *Bristol 642* (COL, DS, GH); near San Francisco, *Cuatrecasas 11541* (COL, F, US); upper part of Río Minchay, Río Mocoa drainage, *Fosberg 20401* (RSA); Portachuelo, valley of Sibundoy, *Schultes & Villarreal 7725* (COL, RSA, US); Sibundoy, *Schultes & Villarreal 7688* (COL, F, GH, NY, RSA, US). RISARALDA: above Santa Rosa de Cabal, Cháquiro-Páramo de Santa Rosa trail, S of Cháquiro Falls, *St. John 20837* (GH, MICH, US). TOLIMA: 47 km W of Fresno on road to Manizales, *Berry 3557* (COL, MO); La Esperanza, Fresno, *Hanbury-Tracy 624* (K). VALLE: above El Guayabo on Palmira-Taco road, *Berry & Escobar 3568* (COL, MO). Palmira, *Duque-Jaramillo 4699* (COL); above La Magdalena, Buga, *Espinal 2057* (MO).

This species is closely allied to *Fuchsia dependens* and *F. hirtella*, based on their predominantly quaternate leaves and paniculate inflorescences. *Fuchsia hartwegii* is the only species with mostly paniculate inflorescences that has short flowers, very narrow petals, and globose fruits.

The species, as treated here, comprises three main geographical groups that may upon further examination warrant recognition as distinct taxa. The first group, including the type collection, is centered around the moist, western, mid-elevation slopes of the Cordillera Central in Cauca, extending as far north as southern Valle and reaching south to Putumayo on the eastern slopes of the same Cordillera. These populations have orange red flowers and are common in roadside thickets, hedgerows, and along streams, where they sometimes occur as lianas.

A second group is found farther north in the Nevado de Ruiz Massif of the Cordillera Central, in Caldas, Tolima, and Antioquia. These plants differ from the first group in their somewhat smaller, cherry red flowers, short-petiolate leaves, and higher altitudinal range. Of the seven collections known from this area, four are male-sterile, *Berry 3557*, *Guarín 3479*, *St. John 20837*, and *Tomás 2406*. Of

the much more numerous collections from the first group to the south, only five male-sterile plants were found, *Haught* 5302, *Lehmann* 5613, *Pittier* 1068, *Schultes* & *Villarreal* 7688, and *Triana* s.n.

A third group consists of collections from the Cordillera Oriental. *Fosberg* 19885 from Huila is very similar to more or less stunted plants that grow in exposed habitats in Cauca, and it is male-sterile. The Cundinamarca collections are all hermaphroditic with mostly fasciculate flowers and differ quite notably from the other groups in having narrow, nearly sessile leaves that resemble those of *F. hirtella*.

Population studies of the different groups discussed above will be required to determine the frequency of male sterility and its relative significance in the breeding system of this species. The finding of male-sterile plants from widely separated localities does suggest that gynodioecy is functioning in at least some populations of *F. hartwegii*. If confirmed, this would be the first report of male sterility in any of the main Andean-Brazilian sections of the genus, which comprise some 75 of the estimated 100 species in *Fuchsia*. Male sterility is presently known only in sects. *Encliandra*, *Kierschlegeria*, *Schufia*, and *Skinnera* (Arroyo & Raven, 1975).

56. *Fuchsia crassistipula* P. Berry, sp. nov. TYPE: Colombia, Dept. Tolima, 40 km W of Fresno on Mariquita-Manizales highway, 2,700 m, 4 June 1979, *Paul E. Berry* 3553 (COL 66345, holotype; MO, isotype). Figs. 18, 36.

Frutex erectus vel scandens 1–3 m altus. Ramuli costati, canescenti-strigulosi. Folia 3–6-verticillata plerumque quaterna, firme membranacea, elliptica vel late oblanceolata basi obtusa vel acuta apice acuta vel acuminata, 6–16 cm longa, 2.5–7 cm lata, superne subvelutina atroviridiaque, subtus pallidioria vel purpurascens sparsim strigosaque; nervis secundariis utroque latere 10–15, margine glanduloso-serrulata et saepe purpurascens; petiolis validis, 2–3.5 mm crassis, 12–40 mm longis; stipulis persistentibus, conspicuis, saepe connatis, subtriangularibus, patentibus recurvatis, 2.5–4 mm longis, ca. 3 mm latis, costa media 2–3 mm crassa (in vivo), in sicco aliquantum minore. Flores roseo-scarlatini, numerosi in racemis (sub-)terminalibus vel paniculis verticillatim racemosis dispositi; rhachidi costata, nutanti, 5–30 cm longa; bracteis 8–20 mm longis; pedicellis 3–8 mm longis; ovario cylindrico, 5–8 mm longo. Tubi florales anguste infundibuliformes, 32–44(–48) mm longi, basi 3–5 mm lati et subnodosi inde 2–3 mm lati constricti superne gradatim dilatati summo 5–8 mm lati, extus strigulosi intus infra medium pilosi. Sepala lanceolata, acuta, 10–14 mm longa, 4–6 mm lata. Petala rubra vel atrorubra, anguste oblongo-elliptica, acuta, mucronata, 11–16(–18) mm longa, 3–5(–6) mm lata. Filamenta rubra, antisepala 7–11 mm longa, antipetala 4–7 mm longa; antheris oblongis, 2.5–3 mm longis, ca. 1.5 mm latis, albis. Stylus roseus glaberque, stigmatibus globosis, apice leviter 4-fisso, 3–4 mm longo, 2–3 mm lato, valde roseo-rubro. Bacca cylindrica, in maturitate subglobosa, 13–15 mm longa, 9–13 mm crassa, viridis vel purpurascens; seminibus inaequaliter oblongo-triangularibus, ca. 1.5 mm longis, 0.8–1.1 mm latis. Numerus gameticus chromosomatum $n = 11$.

Suberect to scandent shrubs 1–3 m tall. Young branches conspicuously 3–6-ridged, one ridge for each leaf in the whorl above, 3–9 mm thick, green, strigillose to subcanescent; older branches terete with dull gray brown, exfoliating bark. Leaves 3–6-verticillate, mostly in whorls of 4 or 5, firmly membranous, elliptic to broadly oblanceolate, acute to obtuse at the base, acute to acuminate at the apex, 6–16 cm long, 2.5–7 cm wide, sparsely strigose and velvety dark green above, strigose and paler to purple flushed below, especially on and along the prominent midrib; secondary veins 10–15 on either side of the midvein; margin glandular-serrulate and usually purple tinged. Petioles stout, 2–3.5 mm thick, 12–40 mm long, sparsely strigose, green to pink red. Stipules conspicuous, subtrian-

gular, divergent, margins and tips recurved on lower nodes, separate to fully connate, thick-callose, 2.5–4 mm long and ca. 3 mm wide when fresh, each stipule with a central longitudinal nerve 2–3 mm thick, considerably flattened and shrunk when dry, persistent. Flowers numerous in terminal or subterminal racemes or verticillately branched panicles; rachis ridged, spreading to drooping, 5–30 cm long; bracts 8–20 mm long. Pedicels short, pendant, 3–8 mm long. Ovary cylindrical, 5–8 mm long, 2–4 mm thick, green, strigose. Floral tube narrowly funnelform, 32–46(–48) mm long, 3–5 mm wide and bulbous at the base, narrowed to 2–3 mm wide above the nectary, then gradually widened above until 5–8 mm wide at the rim, finely strigose outside, pilose inside in lower $\frac{1}{2}$. Sepals lanceolate, acute, 10–14 mm long, 4–6 mm wide, with a short tip 1–2 mm long in bud, spreading at anthesis. Tube subnitid scarlet pink; sepals similar but becoming dull purple towards the tip. Petals deeper red, narrowly elliptic-oblong, acute and $\pm$ mucronate at the apex, 11–16(–18) mm long, 3–5(–6) mm wide, spreading at anthesis. Nectary green, unlobed, ca. 2 mm high, 0.8–1 mm thick. Filaments 7–11 mm and 4–7 mm long; anthers oblong, 2.5–3 mm long, ca. 1.5 mm wide, white. Style glabrous, pink; stigma globose, 4-parted at the apex, 3–4 mm long, 2–3 mm wide, bright red pink, exserted 3–8 mm beyond the anthers. Berry cylindric to subglobose when fully ripe, 13–15 mm long, 9–13 mm thick, nitid green to flushed purple; seeds ca. 1.5 mm long, 0.8–1.1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Central Colombia. Infrequent shrubs in cloud forest thickets of the Nevado de Ruiz Massif in the Cordillera Central, in Depts. Tolima, Quindío, and Caldas; 2,600–3,000 m (Fig. 66).

Specimens examined: COLOMBIA, ANTIOQUIA: Támesis, vicinity of Medellín (Mislabel?), *Toro* 956 (NY). CALDAS: San Félix, near Salamina, *Tomás* 2051 (US). QUINDÍO: Salento to Lagunetas, Old Quindío trail, *Killip & Hazen* 9141 (GH, NY, PH, US); Penares, above Salento, *Pennell* 9195 (GH, PH), 9324 (GH, NY, PH, US). TOLIMA: 43 km W of Fresno on Mariquita-Manizales highway, *Berry* 3554 (COL); La Palmilla, Quindío, Mariquita, *Triana* 3812 (BM, G, K, P, W).

This species is closely related to *Fuchsia hirtella*, which shares the often paniculate inflorescence, short-cylindrical ovaries, glabrous style, and very similar tube and petal dimensions. *Fuchsia crassistipula* is unique in its strongly ridged stems and thick, persistent stipules. The flowers are also more purple than those of *F. hirtella*. All these characters are usually lost upon drying, however, making it difficult to distinguish between the two species in dried specimens. However, *F. crassistipula* has longer, thicker petioles, more serrulate leaves, and often more than four leaves per whorl. Although *F. crassistipula* occurs in the same area as *F. hirtella*, the two are not known to actually grow together.

57. *Fuchsia canescens* Benth. Pl. Hartw. 178. 1845. TYPE: Colombia, Dept. Cauca, near Popayán, ascent to Páramo de Guanacas, 1842, *Theodor Hartweg* 992 (K Benth. Herb., holotype; photograph, MO; BREM, K Hooker Herb., isotypes).

Shrubs 1.5–4 m tall. Young branches ridged, the number of ridges the same as the number of leaves in the whorl above, canescent to hirtellous, reddish, 3–8 mm thick; older branches with tan, exfoliating bark. Leaves 3–5-verticillate,

mostly quaternate, firmly membranous, (narrowly) elliptic to (ob-)ovate, acute to rounded at both ends, 4.5–10 cm long, 2–5 cm wide, medium to dark green and strigillose above, hirtellous to densely strigillose and paler below, with the midvein prominent and reddish; secondary veins 8–15 on either side of the midvein; margin subentire to denticulate. Petioles stout, 15–25 mm long, hirtellous, dull purple. Stipules 0.8–1 mm thick when fresh, lingulate to subterete in transection, subulate at the tip, 1.5–2 mm long, ca. 0.8 mm wide, divergent, occasionally connate, hirtellous, subpersistent. Flowers few to many in upper, leafy nodes or in terminal to subterminal, leafy racemes; rachis 2–10 cm long. Pedicels stout, subtuberculate, pendant, hirtellous-canescens, 5–13 mm long, dull green. Ovary cylindrical, subtuberculate, 10–11 mm long, 3–4 mm thick, hirtellous, light green. Floral tube narrowly funnelform, 34–50 mm long, firmly thick-spongy, 1–2 mm thick when fresh, 3.5–5.5 mm wide and slightly bulbous at the base, narrowed to 3–4.5 mm wide above the nectary, then gradually widened above until 5–9 mm wide at the rim, hirtellous and finely striated-tuberculate outside, densely villous inside in the lower $\frac{1}{2}$ – $\frac{1}{3}$. Sepals similarly thick-tuberculate, triangular, 14–18 mm long, 6–9 mm wide, spreading to divergent at anthesis; buds tetragonous in transection, 1–2 mm wider at the base than the rim of the tube and with small protuberances at the base of adjacent sepals, the tip obtuse or shortly pointed. Tube dull scarlet or orange red, sepals becoming dull white or greenish toward the tip. Petals darker red, subtrullate, 14–19 mm long, 4–7 mm wide, margin slightly undulate, spreading to slightly recurved at anthesis. Nectary light green, irregularly 4-lobed, 1.5–2 mm high, ca. 1 mm thick, often with a few erect, stiff hairs on the top. Filaments red, 9–12 mm and 5–8 mm long; anthers oblong, 3–4.5 mm long, 1.5–2 mm wide. Style orange red, glabrous; stigma capitate, 4-parted at the apex, 2.5–3 mm long, ca. 2 mm wide, red to light pink, exerted 4–9 mm beyond the anthers. Berry ellipsoid, 12–15 mm long, 8–10 mm thick, subtuberculate, green to flushed purple; seeds ca. 1.5 mm long, 0.6–0.8 mm wide. Gametic chromosome number $n = 11$.

Distribution: Southern Colombia. Infrequent shrubs in wet subpáramo or upper cloud forest in Cauca, Huila, and Nariño; 2,800–3,350 m (Fig. 66).

Representative specimens examined: COLOMBIA, CAUCA: 31 km E of Totoró on road to Inzá, *Berry* 3578 (COL, MO); 34 km E of Totoró to Inzá, *Berry* 3579 (MO); 17 km E of Puracé, *Berry* 3581 (COL, MO); Km 56 of Totoró-Inzá road, *Escobar* 1042 (MO); Páramo de Las Papas, between El Boquerón and La Hoyola, *Idrobo et al.* 3918 (COL, P); Paletara to Calaguala, *Pennell* 7083 (GH, NY, PH, US), 7094 (GH, NY, PH, US); Canaan, Mt. Puracé, *Pennell & Killip* 6669 (GH, NY, PH, US); Las Escaleretas, Moras valley, Río Paez basin, Tierra Adentro, *Pittier* 1382 (US); Silvia, Guambía, *Yepes-Agredo* 3078 (COL). HUILA: ca. 40 km E of Puracé to La Plata, *Berry* 3589 (COL, MO). NARIÑO: 31 km E of Pasto on road to Sibundoy, *Berry* 3254 (MO, PSO); Volcán de Sotará, *Lehmann* 6194 (COL).

Because of an incorrectly numbered type collection of *Fuchsia corollata* at Geneva, Munz (1943) thought that *F. canescens* was synonymous with that species. Both *Hartweg* 992 and *Hartweg* 993, the type collection numbers of *F. canescens* and *F. corollata*, respectively, were collected in the same area, so one of the duplicates may have been easily mislabelled. The holotype of *F. canescens* allows no doubt that it is distinct from *F. corollata*. It has dull orange red flowers with thick, firm walls, somewhat tuberculate ovaries and tubes, short pedicels, trowel-shaped petals, and sepals that are tetragonous in bud. It is a very localized and

rather rare species, found only in high elevation cloud forest and subpáramo elfin forests between Cauca and Nariño, and mostly on the east-facing slopes of the Cordillera Central. Though the thick-tubed flowers are characteristic of the *F. denticulata* species group, the generally quaternate leaves, hirtellous pubescence, and mostly racemose flowers place it closer to the *F. dependens* species group, even though it has no close relative in that group. When dried, specimens of this species are likely to be confused with *F. dependens*, but *F. canescens* has fewer, more axillary flowers, ridged stems, stout pedicels, and hirtellous rather than cinereous pubescence.

Berry 3577-B (MO) and *Escobar 1038* (MO) were both collected on the upper eastern slopes of the Cordillera Central in Cauca, at ca. 3,250 m, ca. 31 km E of Totoró on the road to Inzá. Both appear to be hybrids between *F. canescens* and *F. caucana*, species that have similar tube lengths and grow side by side at this locality. *Escobar 1038* has thick flowers typical of *F. canescens*, but the leaves are subsessile, coriaceous, and elliptic, characters that place it closer to *F. caucana*. Its pollen stainability is less than 15% of 500 grains, and that of *Berry 3577-B* is less than 1%. Throughout their range in the Nudo de Pasto, from Cauca to Nariño, *F. canescens* and *F. caucana* are almost always found growing together or nearby. One collection of *F. canescens* was made on the western slopes of the Cordillera Central above Puracé in Cauca, where it was sympatric with *F. corollata*.

58. ***Fuchsia cinerea*** P. Berry, sp. nov. TYPE: Ecuador, Prov. Carchi, just E of the town of Tufiño, 3,210 m, 22 Oct. 1978, *Paul E. Berry 3147* (MO 2737070, holotype; QCA, isotype).

Frutex erectus vel scandens 2–5 m altus, ramulis foliisque junioribus dense cinereo-strigulosus. Ramuli angulati, caulibus teretibus. Folia quaterna vel interdum ternata, membranacea, strigulosa, anguste elliptica, basi acuta apice acuta vel obtusa, 2–5(–7) cm longa, 1–2(–3) cm lata, nervis secundariis utroque latere 5–8(–9) subtus saepe rubrescentes, margine subdenticulata; petiolis 5–12(–20) mm longa; stipulis lanceolatis, 1.5–2 mm longis, ca. 0.5 mm latis, deciduis. Flores axillares, dependentes, plerumque 3–4-verticillati; pedicellis (4–)8–20 mm longis; ovario ellipsoideo vel subpyriformi, 5–8 mm longo, dense cinereo. Tubi florales obscure aurantiaci, infundibuliformes, 42–50 mm longi, basi 3–3.5(–4) mm lati et leviter bulbosi inde 2–2.5(–3) mm lati constricti, superne gradatim dilatati summo 5–6(–8) mm lati, extus striguloso-pilosuli, intus pubescentes. Sepala anguste lanceolata, acuta, 15–19 mm longa, 3–4 mm lata, aurantiaca apice viridescens. Petala aurantiaca vel coccinea, oblonga vel anguste elliptico-lanceolata, 12–15 mm longa, 4–4.5 mm lata. Filamenta antisepala 10–11 mm longa, antipetala 7–8 mm longa; antheris oblongis, eburneis, 2.5–3 mm longis, ca. 1.5 mm latis. Stylus strigosus usque ad summum tubi, stigmatibus globosis apice leviter 4-fisso ca. 2 mm longo, 2–3 mm lato. Bacca ellipsoidea, in maturitate subglobosa, cinereo-velutina, ca. 12 mm longa, ca. 10 mm crassa; seminibus inaequaliter oblongo-triangularibus, 1.7–1.8 mm longis, ca. 1 mm crassis. Numerus gameticus chromosomatum $n = 11$.

Erect to scandent shrubs 2–5 m tall. Young growth densely cinereous-strigillose; branchlets angled, 1–2.5 mm thick; older branches terete, with tan bark. Leaves quaternate or less often ternate, membranous, narrowly elliptic, acute at the base, acute to obtuse at the apex, 2–5(–7) cm long, 1–2(–3) cm wide, matte light green and strigillose above, paler and strigillose below; secondary veins 5–8(–9) on either side of the midrib, usually reddish brown; margin subdenticulate. Petioles strigillose, 5–12(–20) mm long. Stipules lanceolate, 1.5–2 mm long, ca. 0.5 mm wide, deciduous. Flowers axillary, pendant, usually in whorls of 3 or 4. Pedicels strigillose, (4–)8–20 mm long. Ovary ellipsoid to subpyriform, 5–8 mm

long, 2–3 mm wide, densely cinereous. Floral tube narrowly funnelform, 42–50 mm long, 3–3.5(–4) mm wide and slightly bulbous at the base, 2–2.5(–3) mm wide above the nectary, then gradually widened above until 5–6(–8) mm wide at the rim, strigillose to pilose outside, pubescent inside. Sepals narrowly lanceolate, 15–19 mm long, 3–4 mm wide, acute at the apex, spreading at anthesis. Tube and sepals dull orange, sepals with dull green tips. Petals orange to crimson, oblong to narrowly elliptic-lanceolate, 12–15 mm long, 4–4.5 mm wide, obtuse to acute at the apex, spreading at anthesis. Nectary 4-lobed, ca. 1.5 mm high. Filaments orange red, 10–11 mm and 7–8 mm long; anthers oblong, 2.5–3 mm long, ca. 1.5 mm wide, cream. Style strigose from the base to near the rim of the tube; stigma globose, slightly 4-lobed at the apex, ca. 2 mm long, 2–3 mm wide, orange red, exserted 4–10 mm beyond the anthers. Berry ellipsoid to subglobose at maturity, canescent to velutinous, ca. 12 mm long, ca. 10 mm thick; seeds 1.7–1.8 mm long, ca. 1 mm wide. Gametic chromosome number $n = 11$.

Distribution: Known only from the base of Volcán Chiles along the Colombian-Ecuadorian border; 3,100–3,250 m (Fig. 66).

Specimens examined: COLOMBIA, NARIÑO: near village of Chiles, *Camp E-340* (NY, RSA, US), *Wiggins 10580* (DS, POM). ECUADOR, WITHOUT LOCALITY: *Lobb 87* (K).

This species is distinguished by its dense, fine, ashy pubescence, angled stems, small, quaternate leaves, and slender, axillary flowers. It is only known from the adjacent villages of Tufiño and Chiles, on opposite sides of the Colombian-Ecuadorian border, where it grows in secondary thickets at the edge of the towns. This area is not heavily forested and is drier than the opposite side of the Cordillera Occidental. The quaternate leaves, fine, ashy pubescence, and floral dimensions are very similar to those of *F. dependens*, which grows nearby, but has flowers grouped in terminal panicles. *Fuchsia vulcanica* is possibly a related axillary-flowered species that grows close by on the slopes of Volcán Chiles, but at higher elevations; it has coarser pubescence and much wider petals.

59. *Fuchsia triphylla* Linnaeus, *Sp. Pl.* 1193. 1753. Plumier, *Pl. Amer. pl.* 133, *fig. 1*. 1757. Hook., *Bot. Mag. t.* 6795. 1885. Duren, *Rev. Hort. Belge Etrangère* 15:265, *t.* 1889. Watson, *Garden* (London) 41:32, *pl.* 839. 1892. Bosschère, *Ill. Hort.* 43:94, *fig. 10*. 1896. Sieb. & Voss. ex Vilm., *Blumengart.* ed. 3, 1: *t.* 84, *fig. 336*. 1896. Bailey, *Cycl. Amer. Hort.* 2:615, *fig. 877*. 1900. Barker & Dardeau, *Flore d'Haiti* 270. 1930. Essig, *Nat. Hort. Mag.* 13:1, *fig.*, 15, *photo*. 1934. Munz, *Proc. Calif. Acad. Sci.* IV. 25:33, *pl.* 4, *fig. 20*. 1943. Bailey, *Stand. Cycl. Hort.* 1303, *fig. 1606*. 1963. LECTOTYPE here designated: *Plate 14* in Plumier, *Nov. Pl. Amer. Gen.* 1703. Linnaeus simply states the locality as “in America,” but Lamarck (1788) reports that Plumier found the plant in Haiti “dans des lieux incultes, en allant du quartier de la Bande du Sud à celui qu’on nomme de grand Cul-de-Sac.” This locality belongs to the present Département de l’Ouest of Haiti; “la Bande du Sud” probably refers to the southern Massif de la Selle mountain range, and “le grand Cul-de-Sac” is the name of a river originating north of Morne La Visite and flowing northwards, then westwards to Port-of-Prince. Plumier worked in Haiti and Martinique from 1689 to 1697, where he collected objects of natural history and made numerous illustrations of plants. *Fig. 29*.

Fuchsia racemosa Lamarck, Encycl. 2:565. 1788, nom. illeg. based on *F. triphylla* L.; Tabl. Encycl. pl. 282, fig. 1, a–h. 1792. Descourt., Fl. Méd. Antilles 2:161, pl. 109. 1822. non Sessé & Moçino, 1888.

Subshrub to low shrub 3–20 dm tall with erect to drooping branches. Young growth canescent to short pilose; branchlets pubescent, reddish; older branches with tan, exfoliating bark. Leaves opposite or ternate, rarely quaternate, firmly membranous, narrowly lanceolate to elliptic or oblanceolate, acute to narrowly cuneate at the base, acute to acuminate at the apex, 2.5–10(–13) cm long, 1–4 (–5.5) cm wide, dull medium to dark green and strigillose above, pale green to commonly flushed metallic purple and strigose below; secondary veins (6–)7–13 on either side of the midvein, mostly impressed above, elevated and often reddish below; margin subentire to finely denticulate. Petioles pubescent, 4–15(–25) mm long. Stipules lance-linear, 1.5–3 mm long, mostly deciduous. Flowers numerous in suberect to mostly nodding, terminal racemes, occasionally subracemose; rachis 4–12(–15) cm long; leaves subtending the flowers mostly reduced, narrowly lanceolate, and deciduous, but similar to normal leaves if flowers subracemose. Pedicels lightly pilose, 10–30 mm long, divergent to nodding. Ovary ellipsoid, 5–7 mm long, 1.5–2.5 mm wide. Floral tube 25–40 mm long, 2–3.5 and bulbous at the base, sometimes with a ring-like inflation of the tube at the base surrounding the nectary, constricted rather strongly to 1–2.5 mm wide in the lower (6–)10–18 mm of the tube, then abruptly dilated to 8–11 mm wide before narrowing slightly towards the rim; pubescent outside, glabrous inside. Sepals lanceolate, 10–13 mm long, 3.5–4.5 mm wide, spreading at anthesis. Tube and sepals orange to coral red. Petals orange to coral red, elliptic-ovate, rounded to broadly acute at the apex, 6–9 mm long, 4–6 mm wide, suberect to spreading at anthesis. Nectary shallowly 8-lobed, ca. 1 mm high. Filaments orange red, 5–7 mm and 3–4 mm long; anthers oblong, ca. 2.5 mm long, ca. 1.5 mm wide, cream. Style orange red, glabrous; stigma capitate, slightly 4-lobed at the apex, ca. 1.5 mm long and wide, pale red. Berry subglobose to ellipsoid, strigose and $\pm$ 4-angled before maturity, 15–18 mm long, 11–13 mm thick, glossy red purple when ripe; seeds tan, 1.8–2.1 mm long, ca. 1 mm wide. Gametic chromosome number $n = 22$.

Distribution: Endemic to the island of Hispaniola (West Indies); in Haiti, in the southern Massif de la Hotte and Massif de la Selle, in the central Chaîne des Matheaux, and (rare) in the northern range in the Montagnes Noires and Chaîne de Plaisance. In the Dominican Republic, in the southern Sierra de Baoruco, in the central Sierra de Neiba, and in the northern Cordillera Central. Low shrubs on exposed slopes, moist banks, and edges of pine and mixed pine-broadleaf forest; (700–)1,100–2,000 m (Fig. 67).

Specimens examined: HAITI, ARTIBONITÉ: Massif des Cahos, Montagnes Noires, Petite Rivière de l'Artibonité, Pérodin, ridge above Ingrand, *Ekman* 3445 (S). NORD: Citadelle du roi Christophe, on mountain top 5 km SE of Milot, *Bartlett* 17380a (MICH, US). OUEST: Forêt-de-Pins, Massif de la Selle, *Bailey* 185 (BH, US); Massif de la Selle, Morne Franchant, *Ekman* 1170 (K, S, US); Massif de la Selle, Morne Cabaio, near Jardin Bois Pin, *Ekman* 1621 (S); Massif des Matheaux, Grand-Bois, hills towards Toussaint, *Ekman* 5706 (S); Massif de la Hotte, eastern group, Grand Goâve, Morne Calumette, *Ekman* 7339 (G, S); Massif des Matheaux, l'Arcahaie, Habitation Counolle, *Ekman* 9302 (S); Morne des Commissaires, *Holdridge* 850 (MICH, US); le Grand Fond de Port-au-Prince, *Jaeger* 99 (LE); vicinity of Mission, Fond Verettes, *Leonard* 3681 (NY, US), 3701 (NY), 3701a (US). WITH-

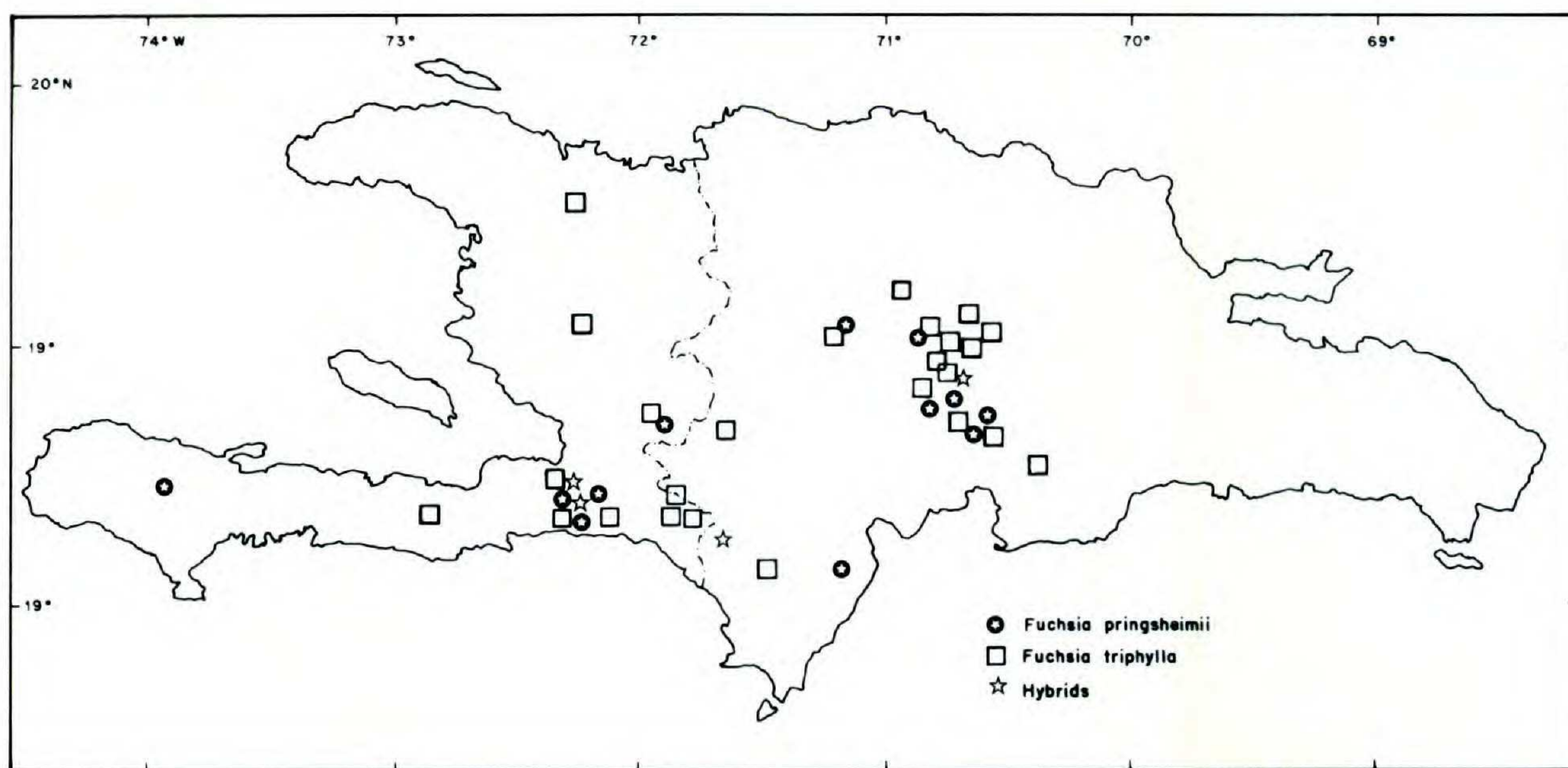


FIGURE 67. Distribution of *Fuchsia triphylla*, *F. pringsheimii*, and naturally occurring hybrids on Hispaniola.

OUT LOCALITY: *Jaeger s.n.* (B, K). DOMINICAN REPUBLIC, AZUA: Loma Nalga de Maco, *Ekman 6304* (S). BAORUCO: without locality, *Howard 12151* (A). LA VEGA: vicinity of Constanza, *Abbott s.n.* (GH, US), *Allard 16446* (US), *Augusto 1150* (A, JBSD), *von Tuerckheim 2956* (BM, F, G, GH, ISC, K, MO, S, U, US, W, Z); between Constanza and Valle Nuevo, *Allard 17422* (US); Jarabacoa, *Augusto 883* (JBSD); Valle Nuevo, *Augusto 1513* (JBSD); El Convento, 10 km S of Constanza to Valle Nuevo, *Berry et al. 3701* (MO, JBSD), *3702* (MO, JBSD); above El Convento, 11 km S of Constanza, *Berry et al. 3703* (MO, JBSD); below La Siberia, new road from Constanza to Valle Nuevo, *Berry et al. 3704* (MO, JBSD); La Siberia, *Berry et al. 3706* (MO, JBSD); S of Jarabacoa, road to Constanza, *Burch & Burch 2546* (CAS, MO); 12 km SE of Constanza, *Davidse 2689* (MO); Loma de Barrero, *Ekman 2057* (G, K); near Jarabacoa, *Fuertes 1619* (A, G, U, W); Río Yaque, *Fuertes 1720* (A, G, W); La Ciénaga, confluence of Río de la Izquierda and Río Los Guanós to form Río Yaque del Norte, *Gastony et al. 149* (GH, US); 8 km S of Constanza, *Gastony et al. 734* (US); Valle Nuevo, *Jiménez s.n.* (DS); Río Grande, Constanza, *Liogier 19453* (JBSD); between Valle Nuevo and Constanza, *Skog 1596* (US); NW of La Ciénaga or La Culata, *Terborgh & Brockman 87* (NA), *88* (NA). PERAVIA: La Nuez, border with Prov. La Vega, *Berry et al. 3712* (MO, JBSD); Sierra de Ocoa, Bejucal, *Ekman H.12039* (A, F, GH, S, US); La Cueva, La Horma Arriba, *Liogier 20999* (JBSD); Plan de Jigüey, *Peña Franjul s.n.* (JBSD). SAN JUAN: Arroyo del Oro, *Canela s.n.* (JBSD), *Howard & Howard 8992* (BM, GH, MICH, S, US). SANTIAGO: Pico de Igua, *Jiménez 1278* (G, US).

This species is easily recognized by its low growth habit, orange flowers, and peculiarly shaped floral tubes. These are nodose at the base, usually strongly constricted in the lower half, then abruptly dilated above the middle, and slightly narrowed again at the rim. *Fuchsia triphylla* can flower when barely woody and just 20–30 cm tall. Its inflorescences are unusual in being nearly erect or nodding in the upper half, although the individual flowers are divergent or drooping as in other species of sect. *Fuchsia*.

Linnaeus based the genus on Plumier's illustration of "*Fuchsia triphylla*, flore coccineo" (Plumier, 1703). It was a fairly crude drawing showing only four stamens, but the unusual floral tube shape clearly identifies the species, and a more complete habit illustration published later (Plumier, 1757) leaves no doubt that Plumier had illustrated the common Hispaniola fuchsia. Even though Linnaeus stated in the second edition of *Genera Plantarum* (Linnaeus, 1742) that the normal number of stamens in *Fuchsia* is eight, he followed Plumier's plate and placed

the species in the Tetrandria Monogynia in the first edition of *Species Plantarum* (Linnaeus, 1753).

Philip Miller (1739) reported having *Fuchsia triphylla* in cultivation at his gardens in Chelsea, England. The seeds were sent to him by William Houstoun, presumably before Houstoun's death in 1733, and said to be from "Carthagera, New Spain." Since Cartagena (it is unclear whether he was referring to Cartagena, Colombia or to a Central American locality) is probably a coastal city, it is very unlikely that it was the actual source of Houstoun's seed. He was known to have travelled in Mexico, Cuba, and Jamaica, but not in Hispaniola. A search of Houstoun's and Miller's collections in the Sloane Herbarium at the British Museum failed to find any specimen of *Fuchsia* (J. Lewis, pers. comm.), so we cannot confirm the identification or date of introduction of what otherwise would have been the first introduction of a living fuchsia into Europe.

Lamarck (1788) tried to change the name of *Fuchsia triphylla* to *F. racemosa*, presumably because he found the triphyllous condition very common among the other, recently discovered species of the genus. Lamarck's name was taken up by Descourtilz (1822), who provided an accurate color illustration of the species in his *Flore Médicale des Antilles*. Descourtilz travelled extensively in Haiti from 1799 to 1803 and worked partly in the mines of the Cibao mountains (Massif de la Selle), where he probably found *F. triphylla*. Surprisingly, he mentions having seen this fuchsia several times in "St.-Jago de Cuba," that is, Santiago, a city on the southeastern coast of Cuba. No other reference of herbarium specimen mentions any native fuchsia on Cuba, however, so he may just have seen cultivated plants there. *Fuchsia triphylla* is listed in his work under "plantes stomachiques astrigentes," used as an antipyretic, decongestant, and as a medication in uterine ailments.

Virtually unknown in Europe during the heyday of fuchsia cultivation and hybridization in the early to mid-1800s, *Fuchsia triphylla* was finally introduced into England in 1882, from seeds collected by Thomas Hogg in Hispaniola in 1873 (Hemsley, 1882). It was then cultivated rather extensively and used in interspecific crosses (Wright, 1978b). It is a rather easy species to grow because it is adapted to considerably warmer temperatures than most fuchsias and flowers when only 2–3 dm tall.

In their native range, plants of *Fuchsia triphylla* exhibit considerable morphological variability. Though they generally have a low growth habit, well-developed and woody shrubs with branches several m long have been collected, such as *Berry et al.* 3706 (MO), from Prov. La Vega, Dominican Republic. Floral tubes generally maintain their unusual shape described previously, but the degree of constriction and the amount of swelling around the nectary varies substantially within local populations. Leaves are particularly variable in their size, shape, and coloration, and some of this variation is associated with geographically isolated populations on the different parallel mountain ranges that traverse Hispaniola. In the southernmost range, the Sierra de Baoruco in the Dominican Republic and the Massif de la Selle in Haiti, the leaves of most collections are firmly membranous and lanceolate, and they occupy the lower extremes of the species limits in size and number of secondary veins. In contrast, plants from the Cordillera Central in the Dominican Republic vary widely, but are generally much larger, thin-

TABLE 19. Comparison of principal morphological characters of *Fuchsia triphylla* and *F. pringsheimii*.

	<i>F. triphylla</i>	<i>F. pringsheimii</i>
Leaf length	2.5–10(–13) cm	1.5–3.5(–4) cm
Petiole length	4–15(–25) mm	1–6 mm
Leaf texture	Membranous	Subcoriaceous
Leaf color	Dull green above, pale to purplish below	Dark glossy green above, white green below
Number of secondary veins	(6–)7–13	3–5
Flower position	Racemose	Axillary
Floral tube length	25–40 mm	19–31 mm
Floral tube shape	Narrowed basally, dilated in the middle, narrowed at the rim	Obconic-funnelform
Flower color	Red orange	Bright red pink
Petal length	6–9 mm	13–24 mm
Petal width	4–6 mm	10–15 mm
Nectary type	Annular, mostly free from the tube	Irregular lobes adnate to the floral tube

ner, and more elliptic than plants from the southern ranges. *Burch & Burch 2546* (CAS, MO) and *Fuertes 1720* (A, G, W) both have leaves reaching 13 cm long and 5.5 cm wide. Plants from this area typically have leaves that are heavily diffused with a purplish coloration, especially on the undersides, but this is by no means ubiquitous in all populations.

Fuchsia pringsheimii is also endemic to Hispaniola. It is morphologically very distinct from *F. triphylla*, as can be seen by a comparison of several morphological characters in Table 19. *Fuchsia triphylla* is much more widespread than *F. pringsheimii*, probably because it is more weedy and occurs at lower elevations. As discussed previously on page 28, the ancestors of these species probably arrived from South America via long distance dispersal. The very marked morphological differences indicate either two separate immigrations or else a wide divergence since the original arrival of a common ancestor. Both species are tetraploid and have biporate pollen, a very unusual combination in the genus, and the two apparently hybridize in nature forming partly fertile hybrids.

A typical altitudinal separation of *Fuchsia triphylla* and *F. pringsheimii* is shown in Figure 5. Although no actual overlap in the altitudinal limits of these species occurs between Constanza and Valle Nuevo, Prov. La Vega, they come very close together around 1,850–1,900 m. A probable hybrid from this approximate altitude was detected, *von Tuerckheim 3541* (BR), in woods below Valle Nuevo, 1,950 m, Aug. 1910. It is intermediate in leaf size, flower position, and flower shape, and has only 30% pollen stainability (400 grains examined). Information on the herbarium label also notes that the plant was growing at an intermediate elevation between populations of *F. triphylla* and *F. pringsheimii*.

A large local population of *Fuchsia pringsheimii* (Berry *et al.* 3712; MO, JBSD) was found interspersed with plants of *F. triphylla* along the edge of a potato field in Dec. 1979 at 2,000 m at La Nuez, on the border of La Vega and

Peravia Provinces in the Dominican Republic. No intermediates or apparent hybrids could be found at that time, but only *F. triphylla* was in flower.

Other hybrids have been detected mostly from Haiti or the Haiti-Dominican Republic border. *Smith & Mejia 10192* (MO, JBSD) is intermediate both florally and vegetatively between the two species; it comes from the Dominican Republic along the Haitian border, Prov. Pedernales, Carretera Internacional between Los Arroyos and Aguacate, in pines at 2,000 m, 10 Nov. 1979. Some of its leaves are 5 cm long with 6 secondary veins (tending toward *F. triphylla*), while the flowers are narrowed in the lower half, yet flare outward at the rim as in *F. pringsheimii*. The petals vary in size from 10 to 16 mm long and 7 to 9 mm wide, intermediate between the two species (see Table 19). The nectary is annular as in *F. triphylla*, and the pollen has numerous aborted, single-porate grains among the plumper bi- and triporate grains. The pollen stainability is 18.7% (500 grains examined). It is interesting that some triporate grains appear here, since both parents have biporate grains. *Jiménez B-4697* (US), from Loma del Toro, in the same province and at the same elevation as *Smith & Mejia 10192*, also shows intermediate morphological characters and has a pollen stainability of under 10%. A final probable hybrid from the Dominican Republic, *Gastony et al. 536* (US), occurs along the Haitian border, but farther north in the Sierra de Neiba at 1,700–2,000 m. It has a pollen stainability of ca. 75%.

In Haiti, *Ekman H.1893* (LL, S) has flowers intermediate between the axillary ones of *Fuchsia pringsheimii* and the racemose ones of *F. triphylla*. It was collected in the Massif de la Selle, Morne Franchant, on the ridge towards Godet, at ca. 1,900 m, Sept. 13, 1920. Except for a slight narrowing toward the rim, its flowers are typical of *F. pringsheimii*, as are the nectaries. The sepals are too short (13–15 mm long) and the petals too small (10–12 mm long and 7–9 mm wide) for that species, however. The leaves of this collection also exceed the normal length for *F. pringsheimii* and have 7 secondary veins. Its pollen stainability is 46.8% (500 grains examined).

Ekman H.1620 (LL, MO, 2 sheets at S, US) is a set of collections in which some specimens appear to be hybrids. The two sheets at S and the one at MO are labelled, "Haiti, Massif de la Selle, Morne Cabaio, near Jardins Bois Pin, ca. 2,000 m, Aug., 1924," but the LL and US sheets say "Marigot" in place of "Morne Cabaio," so it is not clear if they were all collected together. The specimen at S with a typewritten label has numerous, axillary flowers, but constricted floral tubes as in *F. triphylla*. The nectary is an intermediate type between the ring of *F. triphylla* and the adnate nectary of *F. pringsheimii*, and the petals are obovate, but too small for *F. pringsheimii*. Its pollen stainability is 50.4% (500 grains examined). The second sheet at S, with a handwritten label, has flowers shaped much closer to *F. pringsheimii*, with nectaries characteristic of that species. Although its leaves reach dimensions typical of *F. triphylla* (5 cm long, with 7 secondary veins), its pollen stainability is over 90%. The LL sheet has flowers like *F. triphylla* but totally aborted pollen. The MO and US sheets present other combinations of intermediate traits. The wide differences between the different sheets of *Ekman H.1620* may be the result of the segregation of individuals from a hybrid population.

As discussed on p. 31, a single species of hummingbird, *Chlorostilbon swainsonii*, is probably the common pollinator of both *F. triphylla* and *F. prings-*

heimii, and this may help explain the relatively large number of hybrid individuals detected. In addition, severe habitat disturbances have occurred in Hispaniola since the Spanish colonization so that much of the forest vegetation of the island has been eliminated, especially in Haiti (Liogier, 1978). This may have allowed previously separated populations of the two species to enter into closer contact, increasing the chances of intervisitation by *Chlorostilbon*.

60. *Fuchsia pringsheimii* Urban, Symb. Ant. 1:375. 1899. Barker & Dardeau, Flore d'Haiti 270. 1930. Munz, Proc. Calif. Acad. Sci. IV. 25:33, pl. 4, fig. 19. 1943. TYPE: Dominican Republic, Prov. La Vega, near Valle Nuevo, in pines among ferns, 2,100 m, 29 May 1887, *Baron Henrik F.A. Eggers 2159* (B, holotype, destroyed in World War II; BM, G, K, isotypes; photograph of K isotype, MO). Fig. 30.

Erect to scandent shrubs 0.5–2 m tall with ascending to spreading branches. Branchlets terete, puberulent, pruinose, or rarely pilose, reddish purple; older stems with red brown, exfoliating bark. Leaves opposite or ternate, subcoriaceous, narrowly (ob-)lanceolate to elliptic, acute to narrowly cuneate at the base, acute at the apex, 15–35(–40) mm long, 6–15 mm wide, dark rich green and glossy above, subglossy whitish-green to purplish below with red purple veins; upper surface glabrous to loosely strigose, strigose below, especially along the midvein and margin; secondary veins 3–5 on either side of the midvein; margin subentire to glandular-denticulate or dentate, sometimes only toothed in the upper half. Petioles sparsely strigose, 1–6 mm long, red purple. Stipules lanceolate, dark, 1–1.5 mm long, deciduous. Flowers pendant and axillary near the branch tips. Pedicels slender, subglabrous to loosely strigose, 14–40 mm long. Ovary ellipsoid, 6–9 mm long, 2–3.5 mm thick, subglabrous, green to reddish. Floral tube obconic-funnelform, 19–31 mm long, 3–4 mm wide and slightly bulbous at the base, then widened continuously until 9–16 mm wide at the rim, subglabrous outside, glabrous within. Sepals lanceolate, acute to acuminate at the apex, 18–25 mm long, 6–8 mm wide, suberect to spreading at anthesis. Tube and sepals bright red to pink red. Petals red to pink red, broadly obovate, emarginate to broadly truncate at the apex, 13–24 mm long, 10–15 mm wide, slightly spreading and convolute at the base at anthesis. Nectary a yellow-green band lining the basal 2–3 mm of the floral tube, irregularly-lobed and protruding slightly inwards from the tube. Filaments red, 15–18 mm and 12–13 mm long; anthers oblong, 2.5–3 mm long, 1.5–2 mm wide, white to yellow cream. Style red, glabrous; stigma clavate, 4-lobed at the apex, 3–3.5 mm long, 2–3 mm wide, pink to red. Berry oblong, ca. 15 mm long, ca. 8 mm thick; seeds ca. 2 mm thick, ca. 1 mm wide. Gametic chromosome number $n = 22$.

Distribution: Endemic to the island of Hispaniola (West Indies). In Haiti, in the southern Massif de la Hotte and Massif de la Selle ranges and in the central Chaîne des Matheaux, 1,400–2,500 m. In the Dominican Republic, in the southern Sierra de Baoruco, probably in the Sierra de Neiba, and in the Cordillera Central, (1,300–)1,500–2,600 m; low shrubs mostly in pine forests (Fig. 67).

Specimens examined: HAITI, OUEST: Massif de la Selle, Morne La Visite, along path to Saltrou, *Ekman 1450* (US), *1450a* (S), *1450b* (F, G, GH, S); Massif de la Selle, Morne Cabaio road, *Ekman 1613* (S); Massif des Matheaux, Grand-Bois, Morne Moitié-Duportée, *Ekman 5737* (S); Trou Bon

Dieu, Morne La Selle, *Holdridge 1055* (MICH, US). SUD: Morne de la Hotte to mont. Ma Blanche, *Ekman 604* (S). DOMINICAN REPUBLIC, AZUA: Culo de Maco, *Fuertes 1971* (A). BARAHONA: Caña Brava, Monteadá Nueva, *Liogier & Liogier 25126* (JBSD). LA VEGA: Valle Nuevo, *Augusto 1495* (A, JBSD), *1507* (A, JBSD), *Berry et al. 3707* (MO), *3709* (MO, JBSD), *3710* (MO, JBSD), *Bueno (Jiménez Herb. #1792)* (A, US), *Jiménez & Withgow 1382* (US); 16 km S of Valle Nuevo, between La Pirámide and La Nevera, *Berry et al. 3711* (MO, JBSD); Valle Nuevo, Loma Atravesada, *Ekman 13851* (S); trail from Los Tablones (2 km W of La Ciénaga) to La Lagunita, *Gastony et al. 287* (GH); 13 km from Valle Nuevo on road to San José de Ocoa, near the pyramid, *Gastony et al. 716* (GH); Alto de Bandera, *Liogier 25224* (JBSD); near Constanza, *von Tuerckheim 3151* (BM, BR, F, G, GH, K, MO, S, U, US, W, Z). PERAVIA: La Nuez, border with Prov. La Vega, *Berry et al. 3713* (MO); San José de Ocoa, Cuchilla del Pino Atravesado, *Ekman 11710* (K, S); La Cueva, La Horma Arriba, *Liogier 20956* (JBSD). SAN JUAN: Sabana Nueva, Piedra del Aguacate to Río del Oro, *Howard & Howard 9014* (B, BM, GH, LE, S, US).

Fuchsia pringsheimii is characterized by its axillary flowers with wide floral tubes and very large, retuse petals, and by its small, dark green, few-veined leaves. It can be distinguished from *F. triphylla*, the other endemic species on Hispaniola, by the morphological features outlined in Table 19. Both species are tetraploid and apparently hybridize in several different localities, even though *F. pringsheimii* is rather infrequent and occurs at higher elevations than *F. triphylla*. The putative hybrids and their pollinator and ecological relationships are further discussed under *F. triphylla*.

Following Munz (1943), *Fuchsia pringsheimii* is included in sect. *Fuchsia*, but with considerable reservation. Its affinities with this section are doubtful because it has a unique combination of features not found in the main body of sect. *Fuchsia* or in any other groups in the genus. These include the large, convolute, and retuse petals, the sepals nearly as long as the floral tubes, the particular non-annular nectary, the reduced leaves, and tetraploidy with biporate pollen. These characters suggest that *F. pringsheimii* may represent an early offshoot of sect. *Fuchsia* that arrived at Hispaniola via long-distance dispersal from South America, or possibly even an earlier line, that was related to the branch of the genus that may have reached Central America before the close of the Paleogene. The other species of *Fuchsia* on Hispaniola, *F. triphylla*, is also tetraploid with biporate pollen, and the two species hybridize in nature, but *F. triphylla* is morphologically much more similar to the Andean members of sect. *Fuchsia* than is *F. pringsheimii*. Therefore, it is possible that two separate colonizations of the genus occurred in Hispaniola.

Some notable variation in leaf size and pubescence occurs between populations from the Cordillera Central of the Dominican Republic and the southern Sierra de Baoruco and Massif de la Selle. Plants from the Cordillera Central have leaves mostly less than 25 mm long and less than 10 mm wide, with rather short, sparse pubescence. In the southern range, most plants have larger and broader leaves 25–40 mm long and 10–15 mm wide. *Ekman 1613* (S), from Haiti, is heavily hirsute-pilose on both stems and leaves. On the Dominican side of the border in Prov. Barahona, *F. pringsheimii* reaches its lowest altitudinal limit at 1,300 m, according to the label of *Liogier & Liogier 25126*.

61. *Fuchsia verrucosa* Hartweg ex Benth, Pl. Hartw. 178. 1845. Munz, Proc. Calif. Acad. Sci. IV. 25:58, pl. 8, fig. 47. 1943. Rodríguez, Pittiera 6:10, fig. 1, a–e. 1974. TYPE: Colombia, Dept. Cundinamarca, on the road between the

Páramo de San Fortunato and the village of Fusagasugá, 1843, *Theodor Hartweg 991* (K Bentham Herb., holotype; BM, BREM, CGE, K Hooker Herb., LE, OXF, P, W, isotypes; photograph of B isotype, POM). Figs. 28, 35, 46, 47.

Fuchsia perbrevis I. M. Johnston, Contr. Gray Herb. 75:30. 1925. TYPE: Colombia, Dept. Cundinamarca, above Sibaté, 3 Jan. 1854, *Isaac F. Holton 892* (NY, holotype; K, isotype).

Fuchsia verrucosa var. *tamaensis* Steyermark, Fieldiana, Bot. 28:440. 1952. TYPE: Venezuela, Edo. Táchira, base of Páramo de Tamá, between Betania and Tamá, near the Colombian border, 2,430 m, 13 July 1944, *Julian A. Steyermark 57175* (F, holotype; NY, US, isotypes).

Erect to scandent, mostly glabrous subshrubs 0.5–2 m tall. Branchlets subterete, 2–4 mm thick, verrucose, green to dull purple; older stems terete, with light gray tan, finely fissured bark. Leaves opposite, firmly membranous, broadly elliptic to obovate, acute to attenuate at the base, acute to acuminate at the apex, 5–16 cm long, 2–8 cm wide, dark matte green above, pale or flushed purple below, often with strigose hairs along the veins; midvein prominent below, secondary veins 10–20 on either side of the midvein, subparallel and anastomosing 1–3 mm before the margin to form a distinct submarginal vein; margin glandular-serrulate. Petioles stout, 5–22 mm long. Stipules firm to semisucculent, (narrowly) triangular, 2–4 mm long, 1–2 mm wide, separate or connate, subpersistent. Flowers solitary in upper leaf axils. Pedicels firm, spreading to drooping, 10–40 mm long. Ovary oblong-cylindric, tetragonous, 10–12 mm long, 2.5–3 mm wide, lustrous light green. Floral tube obconic, 3–6 mm long, 2.5–3 mm wide at the base, 4–4.5 mm wide at the rim, subglabrous inside and outside. Sepals lance-oblong, acute at the apex, 7–11 mm long, 2–4.5 mm wide at the base, spreading to recurved at anthesis. Tube and sepals bright orange or scarlet. Petals red orange, oblong-obovate, 8–9 mm long, 5–6 mm wide, obtuse to subacute at the apex, margin $\pm$ undulate, central nerve $\pm$ thickened, spreading and convolute at anthesis. Nectary green and composed of 4 distinct antesepalous, ridged lobes ca. 1.5 mm high, ca. 0.5 mm thick, adnate to the base of the floral tube. Filaments light red, 2–3 mm and 1–1.5 mm long; anthers broadly reniform, 1.5–2.5 mm long, 1.5–2 mm wide, white. Style glabrous, stout, red, 6–8 mm long; stigma clavate, slightly 4-cleft at the apex, 2.5–4 mm long, ca. 2 mm wide, light pink to cream, barely exserted beyond the anthers. Berry tetragonous until maturity, ellipsoid or broadly cylindric when ripe, 20–25 mm long, ca. 10 mm thick; seeds 1.4–1.6 mm long, ca. 0.7 mm wide. Gametic chromosome number $n = 22$.

Distribution: Venezuela and Colombia. In the Cordillera Oriental of the Northern Andes from southern Mérida, Venezuela to Huila, Colombia and then on the eastern edge of the Nudo de Pasto in Putumayo; infrequent shrubs in wet, shady banks and along streams; 1,800–3,050 m (Fig. 65).

Representative specimens examined: VENEZUELA, MÉRIDA: road to Mesa de Bustamante, 5 km S of La Playita, between Bailadores and Páramo La Negra, *Tillett & Hönig 738-397* (MO). TÁCHIRA: 6 km E of Zumbador on road to Queniquea, *Berry 3417* (MO); 13 km E of El Portachuelo on road from Bailadores to Pregonero, *Berry 3287* (MO, VEN); 7 km E of El Portachuelo, road to Pregonero, *Berry 3281* (MO), *3662* (MO); El Hato, road to Pregonero, *López-Palacios 1969* (MERF, MO); headwaters of Río Quinimarí, Las Copas, 15 km S of San Vicente de la Revancha, *Steyermark et al. 100577* (MO, VEN); Quebrada Agua Azul, S of El Reposo, *Steyermark & Liesner 118460* (MO, VEN). COLOMBIA, CAQUETÁ: 57 km from Florencia to Altamira, *Luteyn et al. 4954* (COL, MO, NY, US); E of summit between Garzón and Florencia, *Mason 13953* (COL, F, GH, UC, US). CUNDINAMARCA: Barroblanco,

André 1336 (K, NY); Km 34–35 of Bogotá-Sibaté-Fusagasugá road, *Berry 3545* (COL, MO); between Pacho and Río Negro, *García-Barriga 10753* (COL, US); Toquiza, Gazaunta valley, 15 km NW of Medina, *Grant 10260* (COL, NA, RSA); Fusagasugá, *Linden 811* (BM, BR, F, G, K, LE, OXF, W), *Triana 3816* (G, K, P). HUILA: Km 31 of road S of Pitalito towards Mocoa, *Berry 3595* (COL, MO); Gabinete, border with Caquetá, *Cuatrecasas 8465* (CM, COL, F, RSA, US); headwaters of Río Fortalecillas, below Paso de Las Cruces, 39 km E of Neiva, *Fosberg 19787* (RSA, US). META: Páramo de Sumapaz, S of Cordillera de Las Cruces, *Fosberg 20868* (US). NORTE DE SANTANDER: divide between Río La Teja and Río Mesme, between Pamplona and Toledo, *Killip & Smith 19831* (A, F, GH, NY, US), *19976* (A, GH, NY, US); prov. of Ocaña, *Schlim 705* (G, K, P). PUTUMAYO: road from San Francisco to Mocoa, *Mora 4374* (COL); Km 92 from Pasto to Mocoa, *Plowman & Davis 4327* (COL, PSO). SANTANDER: mountains above Bucaramanga, *Barkley & Araque 18S097* (COL, US, VALLE).

This is probably the only species in the genus in which the ovary is clearly longer than the floral tube, and both are quadrangular in transection. It is further characterized by the strictly opposite leaves, verrucose stems, and axillary position of the orange flowers. Vegetatively and geographically, *Fuchsia verrucosa* is consistent with its placement in sect. *Fuchsia*, but its extremely short floral tubes, antesepalous nectary lobes, smooth viscin threads, and tetraploidy with biporate pollen are anomalous in this section. The nectary and small flower size of *F. verrucosa* are most like those of the Central American *F. jimenezii* (sect. *Jimenezia*), but that species has smaller, terete ovaries, paniculate inflorescences, and a reflexed whorl of stamens. *Fuchsia verrucosa* occurs sympatrically with seven other species of sect. *Fuchsia* (*F. cuatrecasasii*, *F. gehrigeri*, *F. hirtella*, *F. nigricans*, *F. scabriuscula*, *F. sessilifolia*, and *F. venusta*), and despite searches in the field and in herbarium specimens, no apparent hybrid plants were found, further indicating a lack of close relatives in sect. *Fuchsia*. Experimental crosses with species such as *F. jimenezii*, *F. pringsheimii*, and other species of sect. *Fuchsia* might help elucidate the affinities of this species.

UNCERTAIN SPECIES

Fuchsia miniata Planchon & Linden, Fl. Serres Jard. Eur. 8:7, pl. 1852. LECTOTYPE: the illustration in the preceding citation, cultivated in Belgium (?) in 1852 by Jean-Jules Linden, from seeds collected in Colombia by M. Schlim.

The illustration and short description provide insufficient detail to characterize this species adequately. Although the illustration closely resembles *F. crassistipula*, the conspicuous stipules of that species are not present in the plate, and the description specifically mentions the stems as terete, whereas in *F. crassistipula* they are conspicuously ridged. A copy of the published illustration is in the herbarium at Montpellier, France (MPU), where Planchon did much of his work. The plate is accompanied in the same folder by several fragments of what appears to be *F. gehrigeri*, but these fragments are not attached to the herbarium sheet and do not seem to correspond to the illustration.

Fuchsia platypetala I. M. Johnston, J. Arnold Arbor. 20:241. 1939. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(4):561. 1941. Munz, Proc. Calif. Acad. Sci. IV. 25:30, pl. 3, fig. 16. 1943. TYPE: Peru, Dept. Apurimac, Chincheros, along lanes in town, semi-cultivated but reported wild nearby, 2,930 m, 1 Nov. 1935,

James West 3705 (UC, holotype, not seen; GH, MO, isotypes; photograph of GH isotype, NY).

This entity is known only from cultivated material from Depts. Apurimac and Cuzco of southern Peru, and no collections more recent than 1946 have been seen. The plants are axillary-flowered with large, obovate petals that are somewhat mottled when dry. They also have reflexed sepals, which strongly suggests a relationship to *Fuchsia boliviana*, a species extensively cultivated nearby, but with long, racemose inflorescences. Other plants referable to *F. platypetala* are *Vargas 6267* (CUZ), from the town of Pumamarca, Dept. Cuzco, 3,400 m, and *Herrera 1514* (GH), from the city of Cuzco. Most likely these represent hybrids of *F. boliviana* with some other axillary flowered species of the region such as *F. denticulata* or *F. austromontana*, both of which have petals that dry streaked or mottled as in the specimens cited above. Whereas the pollen stainability of the type collection is high, the pollen of *Herrera 1514* is totally aborted.

EXCLUDED SPECIES

Fuchsia involucrata Sw., Prodr. 62. 1788. = *Urceolaria involucrata* (Sw.) Standl., N. Am. Flora 32(2):132. 1921. (Rubiaceae).

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